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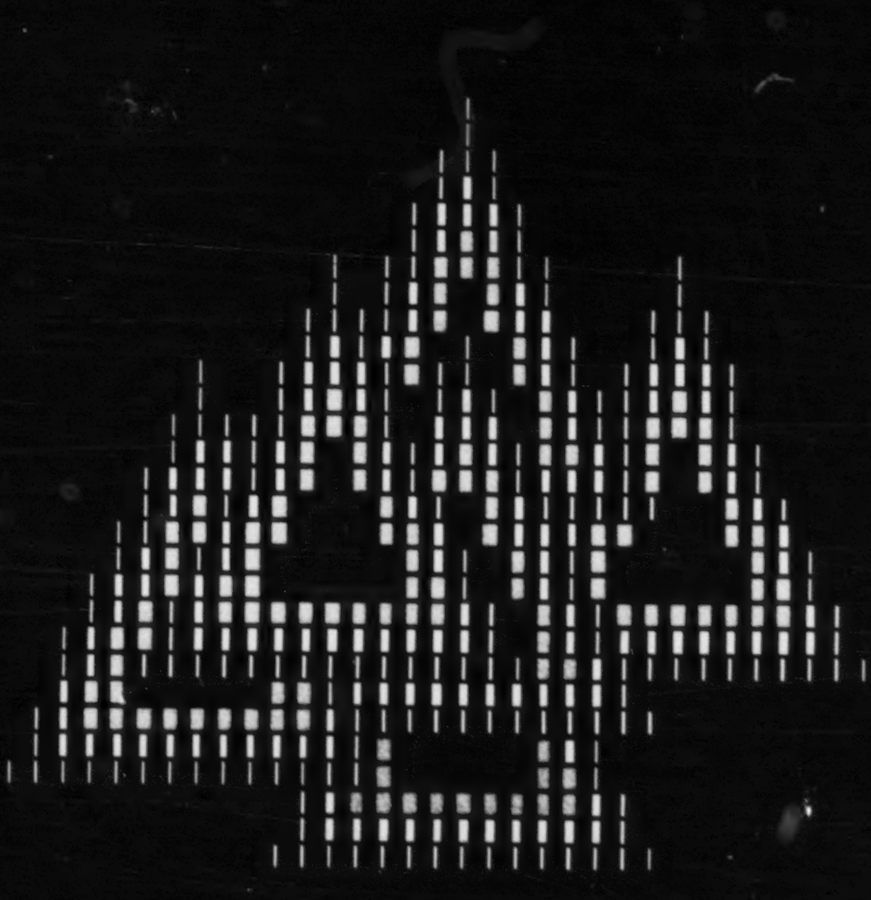
Recent Advances in Spruce Budworms Research

Proceedings of the CANUSA Spruce Budworms Research Symposium



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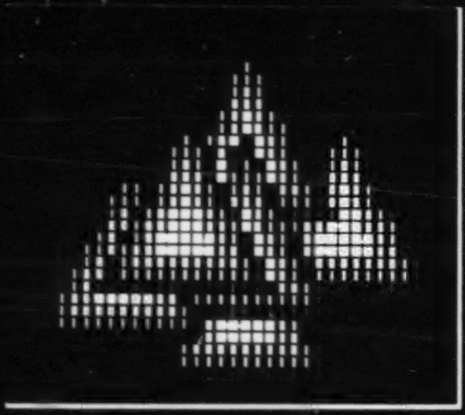

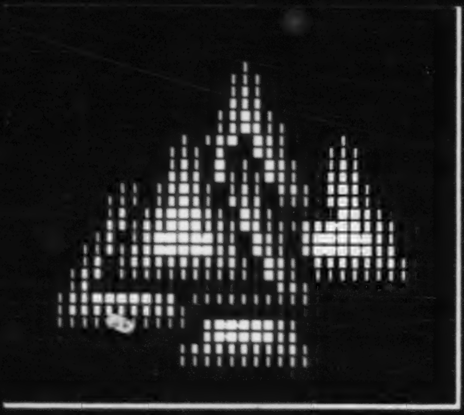

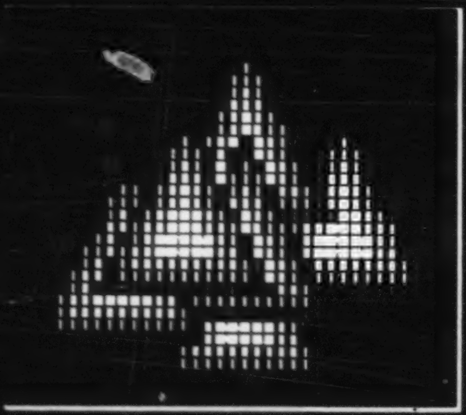

Recent Advances in Spruce Budworms Research

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Entomological Society of America
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Society of American Foresters

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Introduction

In the summer of 1977 the Canada-United States (CANUSA) Spruce Budworms Program was officially ratified by Bob Bergland, Secretary of Agriculture, USDA, and Roméo Leblanc, Minister of the Environment, Canada. This set in motion the planning of a 6-year research, development, and application program with the objective of designing and evaluating economical and environmentally acceptable strategies for controlling spruce budworms and managing budworm-susceptible forests. Scientists and resource managers together drafted a research plan designed to address the problem of reducing the impact of budworms on our forests. Close association of the researchers and the forest managers over the course of the CANUSA Program, permitted the transfer of technology with minimum of formality. A myriad of workshops, demonstrations, leaflets, newsletters, handbooks, publications, and consultations assisted the practitioners to incorporate new and improved tactics and strategies in managing their budworms problems. The Program was designed specifically for the user. Activity schedules and work plan documents were written in terms of anticipated program outputs for the control and management of budworms. Technology transfer was the principle aim.

Notwithstanding the mission-oriented nature of the CANUSA Program, it was recognized very early on by both the Program Leaders and the Joint Policy and Program Council that a wealth of new scientific knowledge would be generated to back the practical direction of the studies and program products. It is therefore not surprising that the Program Management would emphasize the necessity for a final gathering of the program scientists to assemble the new scientific knowledge.

This volume represents a synthesis of the scientific advances achieved during the course of the CANUSA Program. The synthesis papers have been peer reviewed through the auspices of the Society of American Foresters, the Canadian Institute of Foresters, and the Entomological Society of America. Internal reviews have been conducted on the remainder of the contributions.

A program of this nature could only be accomplished with the full cooperation of the scientific community and the leadership of Program Management. Our indebtedness is acknowledged to the Program Manager at Broomall, Penn., Dan Schmitt; the Applications Coordinator Dave Grimble; the Research Coordinator Bob Talerico; the Program Managers at Portland, Oregon, first Max McFadden followed by Ron Stark and Jim Colbert; Application Coordinators Tom Favell and Russ Mitchell and Research Coordinator Jim Colbert; the Canadian Program Managers John Hudak (Newfoundland); Graham Page (New Brunswick); André Lavallée followed by Gilles Frisque (Quebec); Lloyd Sippell followed by Cal Sullivan (Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario); Terry Ennis

Au cours de l'été de 1977, Bob Bergland, secrétaire du ministère américain de l'Agriculture, et Roméo Leblanc, ministre de l'Environnement du Canada, ont officiellement ratifié le programme canado-américain de recherche sur les tordeuses de l'épinette (CANUSA). Ils déclenchaient ainsi la planification d'un programme de recherche-développement et d'applications qui devait durer six ans et dont l'objectif était de mettre au point et d'évaluer des stratégies économiques et écologiques de lutte contre les tordeuses et d'aménagement des forêts vulnérables à ces insectes. Les agents scientifiques et les gestionnaires des ressources ont mis au point en commun un plan de recherche destiné à réduire les dégâts causés par les tordeuses dans nos forêts. Cette collaboration étroite des chercheurs et des gestionnaires, durant l'exécution du programme CANUSA, a permis, avec le minimum de formalités, la dissémination de connaissances techniques. Une foule d'ateliers, de projets de démonstrations, de dépliants, de bulletins, de guides, de publications et de consultations ont aidé les gens du métier à adopter des tactiques et des stratégies nouvelles et améliorées pour maîtriser les problèmes causés par les tordeuses. Le programme était conçu précisément pour les utilisateurs: des calendriers d'activité et des plans de travail ont été rédigés en fonction des résultats prévus du programme, avec comme objectif principal, la dissémination de connaissances techniques.

Nonobstant la nature du programme CANUSA, qui était orienté vers une mission précise, les directeurs du programme et le conseil mixte du programme et des politiques ont reconnu très tôt qu'une masse de nouvelles connaissances scientifiques serait mise au jour pour aider à l'orientation pratique des études et des résultats du programme. Il n'est donc pas surprenant que la Direction du programme ait insisté sur la nécessité de réunir les scientifiques participants, à la fin du programme, pour rassembler cet acquis scientifique.

La présente publication constitue la synthèse des progrès scientifiques réalisés durant le programme. Les documents de synthèse ont été examinés par les confrères des auteurs, sous les auspices de la Society of American Foresters, le Canadian Institute of Foresters et l'Entomological Society of America. Le reste des contributions a été soumis à une révision interne.

Un programme de cette nature ne pouvait être exécuté qu'avec la collaboration entière des milieux scientifiques et que sous l'impulsion de la Direction du programme. Nous sommes redevables au directeur du programme à Broomall (Penn.), Dan Schmitt; au coordonnateur des applications, Dave Grimble; au coordonnateur de la recherche, Bob Talerico; aux directeurs du programme à Portland (Oregon), Max McFadden, en premier lieu, et Ron Stark et Jim Colbert; aux coordonnateurs des applications, Tom Favell et Russ Mitchell et au coordonnateur de la

and Jack Armstrong followed by Errol Caldwell (Forest Pest Management Institute, Sault Ste. Marie, Ontario); Harry Johnson followed by Ben Moody (Alberta); and Doug Miller followed by Tom Sterner (British Columbia). The editing of this volume for scientific content by Chris Sanders and Ron Stark, and for style by Joan Murphy, Martha Brooks, Jim Mullins, and Janet Searcy is also acknowledged with gratitude.

The CANUSA Spruce Budworms Program has been the largest international cooperative forestry project ever attempted, and it has been our honor and pleasure to be associated with it. The lessons we have learned, scientifically and administratively, will undoubtedly stand in good stead in the development of future combined programs. We both thank the scientific community, the forest practitioners, the program management, and the public for the tremendous support that we have received throughout the life of the CANUSA Agreement.

C.H. Buckner
Program Leader
CANADA

M.E. McKnight
Program Leader
USA

recherche, Jim Colbert; aux directeurs du programme canadien, John Hudak (Terre-Neuve), Graham Page (Nouveau-Brunswick), André Lavallée et Gilles Frisque (Québec); Lloyd Sippell et Cal Sullivan (Centre de recherches forestières des Grands lacs, Sault-Sainte-Marie, Ontario); Terry Ennis et Jack Armstrong ainsi qu'Errol Caldwell (Institut pour la répression des ravageurs forestiers, Sault-Sainte-Marie); Harry Johnson puis Ben Moody (Alberta); et Doug Miller puis Tom Sterner (Colombie-Britannique). Nous savons énormément gré, pour la révision scientifique de la publication, à Chris Sanders et à Ron Stark, et, pour le style, à Joan Murphy, Martha Brooks, Jim Mullins et Janet Searcy.

Le programme CANUSA a été le plus important projet international de collaboration dans le domaine forestier jamais lancé, et nous avons été très honorés et très heureux d'y être associés. Les leçons que nous en avons tirées, sur les plans scientifiques et administratifs, profiteront énormément, à n'en pas douter, à l'élaboration de programmes mixtes ultérieurs. Nous remercions les milieux scientifiques, les forestiers, les gestionnaires du programme et le public pour l'aide considérable qu'ils nous ont accordée durant le programme CANUSA.

C.H. Buckner
Directeur du programme
au Canada

M.E. McKnight
Directeur du programme
aux États-Unis

Welcoming Remarks
Allocution de bienvenue

It is a privilege for me to comment briefly at the start of the Spruce Budworms Symposium. This symposium is both the end of one program and the beginning of other cooperative forestry activities. The symposium is the last major activity in a program developed to coordinate research on the spruce budworms. This research has been accomplished under a formal agreement between the United States and Canada; as a result the CANUSA Program has been a great success. The Spruce Budworms Program is now coming to an end but the cooperative work between the two countries is continuing. Additional answers to the budworms problem will be obtained as well as cooperative research on other forestry problems. The cooperative research completed during the budworms program was only the start of such cooperation.

The symposium presented here is the result of long hours of work by many people. The program managers Melvin McKnight from the U.S and Charles Buckner from Canada were supportive throughout. The symposium program itself was planned and monitored by Christopher Sanders from Canada and Ronald Stark from the United States, who spent many hours to assure that all speakers would be prepared for the Bangor meeting. Three others were active in putting together a very fine poster session; David Grimble and Russel Mitchell from the U.S. and Robert Taylor from Canada. Those mentioned are only a few of the many who have worked long hours to provide a symposium that is complete and interesting for those attending. I hope that those who read the proceedings will be pleased with the information provided.

It is my pleasure as general chairman to present our two lead speakers who will speak on "CANUSA beginning to end." Dr. Keith R. Shea, Associate Deputy Chief for Research, U.S. Department of Agriculture, Forest Service will speak for the United States. Dr. Carl H. Winget, Director General, Research and Technical Services, Canadian Forestry Service prepared the Canadian comments which will be presented by Dr. George Green in his absence.

***F.B. Knight,** General Chairman*

(Associate Dean, College of Forest Resources, University of Maine at Orono, Orono, ME)

Pour moi, c'est un privilège de vous faire part rapidement de mes observations, en ce début du colloque sur les tordeuses. Trait d'union entre l'aboutissement du programme et le début de la collaboration en foresterie, ce colloque couronne un programme lancé pour coordonner la recherche sur les tordeuses. Cette recherche a été réalisée en vertu d'une entente officielle entre les États-Unis et le Canada, qui a garanti le succès du programme CANUSA. Le programme prend bientôt fin, mais la collaboration entre les deux pays se poursuivra. Des réponses supplémentaires aux problèmes des tordeuses seront obtenues, et des recherches en collaboration viseront d'autres problèmes touchant les forêts. La recherche menée en collaboration durant le programme n'était que le début d'une telle collaboration.

Le présent colloque est le résultat de longues heures de travail et beaucoup de personnes y ont mis la main. Dès le début, les responsables Melvin McKnight, des États-Unis, et Charles Buckner, du Canada, ont prêté leur appui. Le programme du colloque a lui-même été planifié et contrôlé par Christopher Sanders, du Canada, et Ronald Stark, des États-Unis, qui ont consacré de nombreuses heures pour faire en sorte que tous les conférenciers soient prêts pour la réunion de Bangor. Trois autres personnes ont grandement travaillé à monter une excellente session de présentation sur posters: David Grimble et Russel Mitchell, des États-Unis, et Robert Taylor, du Canada. Ceux que j'ai mentionnés ne sont qu'une poignée parmi tous ceux qui ont consacré de longues heures afin que le colloque intéresse tous les participants et répondent à tous leurs voeux. Je souhaite que ceux qui liront les comptes rendus seront satisfaits des renseignements qu'ils y trouveront.

En tant que président général, il me fait plaisir de vous présenter nos deux principaux conférenciers qui nous feront l'historique du programme CANUSA: M. Keith R. Shea, sous-chef adjoint de la recherche, au Service des forêts du ministère américain de l'Agriculture, et M. George Green, qui présentera les observations préparées par M. Carl H. Winget, directeur général de la Recherche et des Services techniques du Service canadien des forêts, absent.

***F.B. Knight,** président général*

(Doyen adjoint, College of Forest Resources, University of Maine at Orono, Orono, ME)

CANUSA — In the Beginning
Les débuts de CANUSA

K.R. Shea

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CANUSA had its beginning in the year of the great snows — MCMLXXVII–VIII. For many years, a horrendous plague had been visiting upon the forest lands of USA and Canadia. The peoples of these lands had raised a great outcry which fell upon the ears of the Pharaohs in the temples of Washingtonia and Ottawania. For years the Pharaohs of these two lands had poured out much gold from their treasure houses. They had sprayed many hectares with poisonous substance to no avail. The plague had continued; the forests were devastated; and the cries of the people mounted in furor. The Pharaohs of the two lands were agitated — "We have a rebellion on our hands. What should we do?" The Pharaohs in their infinite wisdom summoned their two Oracles (Buckman and Bourchier). Great debates ensued in Washingtonia and Ottawania. Very few dinars remained in the treasure houses and the outlook for more gold was dim. Finally, at a great meeting of the Pharaohs, it was decided, "We'll pool our resources. This plague is more than we can handle alone."

So it came about that four Apostles (Harris, Stewart, Shea, and McKnight) journeyed from the USA southland, through snow and ice, to the cold northland to meet with the Canadia Apostles. The meeting was held in the frigid village of Sault Ste. Maria.

During the first day of the meeting, the USA Apostles outlined a great program planning technique — ACTAR. ACTAR had saved the USA from other plagues — the moth of the gypsy, the moth of the tussock, and the scarab beetle of pinus. Surely, the USA Apostles exclaimed, ACTAR can save us all from this latest plague — the worms of picea. Although my memory is dim, there are two worms of picea — one in the East and one in the West.

Then there arose a great debate among the Apostles from Canadia. "How can our Pharaoh do this to us?" "He's out to get us!" "I'll quit, etc., etc., etc." echoed throughout the catacombs of Sault Ste. Maria. With great fear and trepidation, so ended the first day.

But the Pharaoh from Canadia was a wise Pharaoh. He prepared a great feast for all the Apostles from USA and Canadia. Although a few debates and an occasional cry of outrage occurred, the evening was a joyous occasion. Bawdy songs were sung and the Apostles from the two great lands walked down the streets of Sault Ste. Maria arm in arm.

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CANUSA a débuté l'année des grandes tempêtes hivernales de MCMLXXVII–VIII. Depuis plusieurs années, un terrible fléau s'abattait sur les forêts de l'USA et de CANADIA. Les habitants de ces régions avaient lancé des cris de lamentations qui étaient parvenus aux oreilles des Grands Prêtres dans les temples de Washingtonia et d'Ottawania. Depuis plusieurs années, les Grands Prêtres de ces deux pays avaient versé beaucoup d'or puisé à même leurs réserves pour combattre ce fléau. Ils avaient subventionné l'épandage de poisons sur des millions d'hectares de forêts sans résultat satisfaisant. Le fléau persistait, les arbres périssaient, et les plaintes des habitants des deux pays s'amplifiaient. Les Grands Prêtres s'inquiétèrent: «Nous faisons face à une révolte. Comment pouvons-nous la régler?» Dans leur sagesse, les Grands Prêtres firent appel à leurs deux oracles (Buckman et Bourchier). De sérieuses délibérations s'ensuivirent à Washingtonia et Ottawania. Les coffrets se vidaient, les dinars se faisaient de plus en plus rares et les perspectives d'obtenir plus d'or n'étaient pas réjouissantes. En dernier lieu, lors d'une réunion plénière les Grands Prêtres déclarèrent d'un commun accord: «Nous allons nous unir pour combattre ce fléau que nous ne pouvons vaincre séparément».

Voici que les quatre apôtres (Harris, Stewart, Shea et McKnight) quittèrent l'USA, terre du sud, et se dirigèrent à travers glaces et neige vers le nord pour rencontrer les apôtres de Canadia. La réunion pris place dans le froid village de Sault-Sainte-Maria.

Au cours de la première journée, les apôtres de l'USA présentèrent un programme basé sur le programme ACTAR. ACTAR avait sauvé l'USA de fléaux antérieurs — la spongieuse, la chenille à houppes du douglas et le scarabée des pins. À coup sûr, les apôtres de l'USA s'exclamèrent, ACTAR peut nous sauver du présent fléau, les chenilles de l'épicéa. Quoique ma mémoire soit vacillante, je crois qu'il existe deux espèces de chenilles de l'épicéa, une de l'Est et une de l'Ouest. Un grand débat s'ensuivit parmi les apôtres de Canadia. «Comment notre Grand Prêtre peut-il nous imposer cela?» Ces gémissements se faisaient entendre d'un bout à l'autre des catacombes de Sault-Sainte-Maria. La première journée prit fin dans un sentiment d'inquiétude et de trépidation.

Mais le Grand Prêtre de Canadia était imbu de sagesse. Il convoqua tous les apôtres de l'USA et de Canadia à un plantureux festin. Bien que quelques discussions et un occasionnel cri d'outrage se fissent entendre, la soirée se passa dans la joie.

And so, on the second day it was proclaimed — "We will band together in this fight against the plague that persists in the forests of the lands of Canadia and USA."

"What shall we call this band?" a Subpharaoh queried. A great hush fell over the Apostles from Canadia and USA. Finally, one Apostle spoke up. "Let's call this band, USACAN." After much debate it was decided that USACAN was a bit obscene and might offend the gods. "How about CANUS?" This touched a tender nerve among the Apostles from Canadia. For the past two years, following a great dinar famine, many of the Apostles from Canadia had been eliminated. Many heads had rolled as the Pharaoh's guillotine worked night and day. So "CANUS" was dropped. Finally, someone shouted "Why not CANUSA?" A great silence followed. The drip-drip of water from melting icicles on the eaves of the catacomb could be heard. No one could think of anything better.

The naming of CANUSA caused great jubilation in the temples of the Pharaohs in Ottawania and Washingtonia. Surely, now all was well. But someone noted there was no implementation plan — a necessity in all pharaohcratic systems. Finally, the two Pharaohs decided there must be a Tablet of MOU. And, so it came to pass, that two Apostles, Babcock from Canadia and Shea from USA, met in Washingtonia. There on the shores of the great POTOMAC, they chiseled in stone a Tablet of MOU. In due course, the two Pharaohs of the two lands, Canadia and USA, affixed their seals confirming the great alliance and the CANUSA Program was born.

You may think this is the end. But, NO, there is more to come.

Now the Pharaohs and Subpharaohs in Washingtonia and Ottawania, having appeased the dwellers of the forests in USA and Canadia, felt free to leave their temples and mingle with the people. Once again, the Pharaohs summoned their Oracles. Much thought and gazing at crystal balls ensued. Finally, it was decided to form two great groups to oversee CANUSA. The two groups became known as the JPPC and the JPU. This provided an opportunity for the Pharaohs and Subpharaohs to travel about their Pharaohdoms to see new sights and to visit.

At about the same time, two Managers of Programs were named — Apostle McKnight (USA) and Apostle Buckner (Canadia). Thereafter, they were known as the Priests of the High Court of the Pharaohs — men who were feared and bowed to upon every occasion. It is said that the greater the appearance of fear and the more humble the bows, the greater the dinars allotted to the subpriests and working Apostles. Having not witnessed this phenomena, I can only report on what I have heard.

Des chansons paillardes retentirent et les apôtres des deux grands pays marchèrent bras dessus, bras dessous dans les rues de Sault-Sainte-Maria.

Voici qu'au cours de la deuxième journée on proclamait: «Nous allons nous unir et former une ligue pour lutter contre ce mal qui s'acharne sur les forêts de Canadia et de l'USA».

«De quel nom désignerions-nous cette ligue? demande un acolyte. Après un long silence, un apôtre se fit entendre: «Nommons cette ligue USACAN». Après discussion il a été convenu que USACAN était un peu grivois et que cette appellation pourrait offenser les dieux. «Que penseriez-vous de CANUS?» Ceci semblait déplaire aux apôtres de Canadia. On se souvenait qu'à la suite d'une grande disette de dinars, de nombreux apôtres de Canadia avaient été congédiés au cours des deux dernières années. Plusieurs têtes étaient tombées lors du travail inlassable de la guillotine du Grand Prêtre. Donc, «CAN US» fut mise de côté. Finalement, quelqu'un cria: «Pourquoi pas CANUSA?» Un silence profond s'ensuivit. On pouvait entendre dégoutter les glaçons qui fondaient le long du toit des catacombes. Personne ne pouvait trouver mieux Cette appellation de CANUSA fut la cause de jubilations dans les temples des Grands Prêtres à Ottawania et Washingtonia. On pouvait enfin dormir en paix. Toutefois, on s'aperçut qu'il manquait un plan d'exécution — une nécessité dans tout système autocratique. Finalement les deux Grands Prêtres décidèrent qu'il faudrait façonner une table de lois. Ceci donna suite à une rencontre à Washingtonia des Apôtres Babcock de Canadia et Shea de l'USA. Sur les rives de l'imposant POTOMAC, ils ciselèrent sur pierre une table de lois. Finalement, le Grand Prêtre de Canadia et celui de l'USA apposèrent leurs sceaux certifiant cette historique alliance qui donnait naissance au programme CANUSA.

Vous pouvez penser que c'est la fin de l'histoire; mais non, il y a une suite.

Après avoir apaisé les habitants des forêts de l'USA et de Canadia, les Grands Prêtres et leurs acolytes de Washingtonia et d'Ottawania prirent la liberté de quitter leurs temples pour se mêler à la populace. Une fois de plus, les Grands Prêtres firent appel à leurs oracles. À la suite de nombreuses incantations et après avoir scruté les boules de crystal, la décision fut prise de former deux groupes pour la surveillance de CANUSA. Ces deux groupes devinrent le CMPP et GMP. Ces institutions fournirent l'occasion aux Grands Prêtres et à leurs acolytes de parcourir leurs domaines, de se rendre visite et de découvrir de nouveaux horizons.

C'est à cette époque que deux gestionnaires de programme furent nommés — l'apôtre McKnight (USA) et l'apôtre Buckner (Canadia). À partir de ce moment, ils furent reconnus comme les Prêtres de la Haute Cour

At about this time, the Apostle Shea was exiled to the hinterland of the great Pharaoh of SEA. So my story of how CANUSA began must end. The archives in Washingtonia and Ottawania may not verify what I have remembered here. But this is the way it really was.

There may be other versions of The Beginning. Some of these you may have heard around the campfires in the wilds of Canadia and USA, where the old gray beards gather to spin yarns. It is in this way that legends are born.

des dirigeants — des hommes à craindre et à vénérer en tout temps. On a cru s'apercevoir que plus les manifestations de soumission étaient marquées et plus les courbettes étaient profondes, plus l'octroi de dinars était généreux pour l'accomplissement des travaux par les apôtres. N'ayant pas été témoin de ces faits, je ne peux que rapporter les ouï-dire.

À cette époque, l'Apôtre Shea fut exilé dans le bled du Patriarche de SEA. C'est pourquoi je dois mettre fin à mon récit des débuts de CANUSA. Les archives de Washingtonia et d'Ottawania ne confirmeront peut-être pas tout ce que je viens de relater. Cependant, c'est ainsi que les choses se passèrent.

Il pourrait y avoir d'autres versions de ce début de CANUSA. Vous en avez peut-être entendu raconter autour des feux de camps dans certains bleds de Canadia et de l'USA, où les vieillards à barbes grises se rassemblent pour raconter des histoires. C'est ainsi que naissent les légendes.

CANUSA: Beginning to End
Le programme CANUSA à son crépuscule

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Introduction

Dr. Shea has brought you through the early planning stages of this joint venture, up to the point when the agreement was signed and the program activated. I will carry the torch from there, to bring you to the present and in two weeks, the end of the CANUSA Program. I will not attempt to catalog the scientific achievements of the Program; these will be evident over the next four days. Instead, I will attempt to give you a manager's perspective of the program we created, the unique problems that were presented to us, and some of the solutions we arrived at to integrate the combined forces of the United States and Canada into a workable scientific unit to address the common problem of spruce budworms in North America.

As one looks at the 1983 and 1984 infestation and damage maps of budworms, it comes as no shock that in both west and east, the budworm is still a formidable foe. As Dr. Tom Angus, former Director of the Insect Pathology Research Institute of the Canadian Forestry Service, and one of the founders and backers of CANUSA so frequently put it, the budworms march on. And they do! And they obviously haven't heard of CANUSA! But CANUSA has heard of the budworms! There have been critics that have told us that the solution to the problem is to cut all impacted stands, convert those stands into paper, and with the products, publish CANUSA documents. I don't know how this argument relates to our mutual acid rain problem but if we look far enough I am sure that we can discover a parallel. However, having acknowledged that the budworms are still with us, I think you must agree that at the very least, we have discovered a few more chinks in their armor, and that we are in a better position to deal with the problem than we were in 1977 when the formal CANUSA agreement was signed. We knew at the beginning that there would be no quick and ready solutions, but we felt that we could provide the resource managers with better tactics and alternatives. Technology transfer activities from the CANUSA Program give me the feeling that, to a degree, this has been accomplished. I say to a degree, because what follows CANUSA is probably as important as what has taken place in its 7 year life span. The rapport that has developed between the scientists at the working level has no doubt provided us with a legacy of cooperative and integrated research that will persist long after CANUSA had ended. But that is the future, and my

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Introduction

M. Shea vous a fait l'historique de l'avant-projet de cette entreprise commune, jusqu'à la signature de l'accord et au déclenchement du programme. C'est ici que je prend la relève pour vous faire l'historique final du programme CANUSA qui prendra fin dans deux semaines. Je ne tenterai pas de cataloguer ses réalisations scientifiques; elles seront évidentes au cours des quatre prochaines journées. Je tenterai plutôt de vous présenter le programme que nous avons créé selon la perspective d'un gestionnaire, les problèmes inédits que nous avons eu à résoudre et certaines des solutions que nous avons trouvées pour intégrer les forces scientifiques américaines et canadiennes dans un tout discipliné, capable de s'attaquer au problème commun des tordeuses en Amérique du Nord.

Devant les cartes des dommages et des infestations des tordeuses, en 1983 et 1984, on constate facilement que, dans l'Ouest et dans l'Est, la tordeuse reste un ennemi redoutable. Comme le disait si souvent Tom Angus, ex-directeur de l'Institut de recherche en pathologie des insectes du Service canadien des forêts et un des fondateurs et piliers du programme CANUSA, les tordeuses ont le vent dans les voiles. Et c'est vrai! Elles n'ont visiblement pas entendu parler du programme CANUSA! Mais nous, nous avons entendu parler d'elles! Les critiques nous ont donné comme solution au problème de raser tous les peuplements infestés, d'en transformer le bois en papier qui servirait à publier des documents sur le programme CANUSA. Je ne sais pas comment cette solution se rattache au problème commun des pluies acides, mais si nous regardons suffisamment loin, je crois que nous pouvons découvrir un parallèle. Toutefois, après avoir constaté que les tordeuses n'ont pas disparu, vous conviendrez sans doute qu'à tout le moins nous avons découvert quelques défauts de plus dans leur cuirasse et que nous sommes mieux équipés pour nous attaquer à elles qu'en 1977 lorsque l'accord CANUSA a été officiellement signé. Au départ, nous savions qu'il n'y aurait pas de solution rapide et toute trouvée, mais nous pensions pouvoir transmettre aux aménagistes de meilleurs moyens de lutte et de meilleures solutions de rechange. Les échanges de connaissances techniques dans le cadre du programme me font croix que, jusqu'à un certain point, cet objectif a été atteint. Je dis jusqu'à un certain point parce que ce qui succédera aux 7 années CANUSA est probablement aussi important. Les relations professionnelles établies entre les chercheurs nous ont sans doute fait hériter

mandate here is to bring you to the end of the CANUSA agreement. So let us talk about the beginnings of the formal working relationships that have brought us through to this point in the evolution of the CANUSA Program.

The Administrative Structures

When Bob Bergland, U.S. Secretary of Agriculture, and Romeo Leblanc, Canadian Minister of the Environment, added their signatures to the Memorandum of Understanding that formalized the joint budworm research, development, and application program, they left it to their respective staffs to mold two dissimilar organizations into an efficiently functioning unit. There were many basic differences, such as the fiscal calendars of both countries were not in phase: the USA fiscal year runs from October 1 to September 30, whereas the Canadian counterpart runs from April 1 to March 31. Talking about budgets is difficult when they are six months out of step. The funding process was different on each side of the international border: the USA program was funded mainly by accelerated funds over a specified term with a relatively low level of base funding, while the Canadian program was effected principally by restructuring the base program and with very little additional funding input. This arrangement was difficult for many scientists to understand. Also lines of authority that existed on each side were not the same.

In the USA, the base budworm research program was located at the Intermountain, North Central, Northeastern, Pacific Northwest, and Rocky Mountain Stations, as well as in the many State and Private Forestry Areas. Blanketing if not swamping this existing structure, there was added an accelerated program, administered at the Northeastern and Pacific Northwest Stations under the direction of two program managers through the Program Leader in Washington.

In Canada, what "accelerated" funds were available, were channeled through the office of the Program Leader in Ottawa, and the research program itself was under the direction of the regional establishments in St. John's, Newfoundland; Fredericton, New Brunswick; Sainte-Foy, Quebec; Sault Ste. Marie, Ontario; Edmonton, Alberta; and Victoria, British Columbia. Two institutes, the Forest Pest Management Institute at Sault Ste. Marie and the Petawawa National Forestry Institute also participated. The National Forest Insect and Disease Survey program played a lead role on many aspects of the damage appraisal and forecasting studies included in the program.

To knit all these various and isolated components together into an integrated and cohesive research and

d'une recherche intégrée et d'une collaboration qui dureront longtemps après la fin du programme. Mais cela, c'est l'avenir, et mon mandat est de vous transporter jusqu'à la fin de l'entente CANUSA. Parlons donc des débuts des relations de travail officielles et de l'évolution du programme.

Les structures administratives

Lorsque Bob Bergland, secrétaire américain de l'Agriculture, et Roméo Leblanc, ministre d'Environnement Canada, ont signé le mémoire d'intention qui a officialisé le programme d'application, de développement et de recherche sur les tordeuses, ils ont laissé à leur personnel respectif le soin de faire de deux organismes dissemblables une unité efficace. Les différences fondamentales étaient nombreuses: aux États-Unis, l'année financière va du 1^er^ octobre au 30 septembre, au Canada, du 1^er^ avril au 31 mars (ce décalage de 6 mois complique les discussions budgétaires); le programme américain a surtout été financé de façon accélérée, pendant une période déterminée, le financement de base étant relativement faible, tandis que le programme canadien a surtout été réalisé par la restructuration du programme de base et un financement supplémentaire modeste. Pour beaucoup de chercheurs, ces modalités étaient difficiles à comprendre. De plus, dans chaque pays, la hiérarchie n'était pas la même.

Aux États-Unis, le programme de recherche sur les tordeuses était fondamentalement limité aux stations des Rocheuses, du Nord-Ouest du Pacifique, du Nord-Est, du Centre-Nord et de l'Intermountain ainsi que dans de nombreuses régions forestières privées et étatiques. Chapeautant cet édifice, s'il ne l'alourdissait pas, un programme accéléré était géré dans les stations du Nord-Est et du Nord-Ouest du Pacifique, sous la direction de deux gestionnaires par le truchement du directeur de programme à Washington.

Au Canada, ce qu'il y avait de financement accéléré disponible était distribué à partir du bureau du directeur du programme à Ottawa, et le programme de recherche proprement dit relevait des établissements régionaux de Saint-Jean de Terre-Neuve, de Fredericton, de Sainte-Foy, de Sault-Sainte-Marie, d'Edmonton et de Victoria, et de deux instituts, celui de la répression des ravageurs forestiers à Sault-Sainte-Marie et l'institut forestier national de Petawawa. Le programme national du Relevé des insectes et des maladies des arbres a joué un rôle crucial dans beaucoup d'aspects du programme CANUSA touchant la prévision et l'évaluation des dommages.

Intégrer cet assemblage d'éléments disparates en un programme cohérent de recherche et de développement constituait une tâche herculéenne, qui exigeait development program was a herculean task, commanding much of our ingenuity and resources. The Program Leaders devised an "Activity Schedule" that was published annually after approval by senior program administration. The Activity Schedule encapsulated the various program elements, arranged these in subject matter order, and tracked the intended and actual progress of each facet of the Program.

The CANUSA Program, as it existed in 1977 was quite diffuse, with elements in the two sponsoring services, in state and provincial programs, in universities, and in the private sector. To take stock of the state of the art, the two Program Leaders accepted as one of their first tasks the assembly of a comprehensive inventory of budworms research. The inventory, recognized as being only as good as the input to it, has been maintained throughout the life of the Program. It acted as a yardstick for measuring progress and provided a framework upon which new studies could be cataloged. It is interesting that studies that had been missed in the existing Program were surfacing up to and including the final inventory publication. Over the life of the Program some have said the inventory tomes have competed, perhaps with more success that we care to admit, with the budworms for fir and spruce fiber!

The Joint Policy and Program Council (JPPC) and the Joint Planning Unit (JPU) functioned throughout the life of the agreement as the senior policy authority and the scientific program authority respectively. Each unit was comprised of 8 members, four from each country. Both groups met at least once each year during the Program, and in the latter part of the Program, they began meeting together. There have been criticisms that the Program was over administered, but the fact is the resolution of policy matters by the JPPC and the critiques of the program by the JPU were greatly facilitated by the actions of these two groups.

Each year the progress of the Program was reviewed, compared with the projections of the Activity Schedule, and cost accounted. The Program Leaders, in cooperation with their Program Managers, assembled the Program documentation and laid out plans for the Program and Budget for the coming year. It was the responsibility of the JPU to review the documents and to bring to the attention of the JPPC the strengths and weakness in the planning and execution of the work. Sensitive issues such as environmental and human health aspects, cross border policy impacts, and publicity and public relations matters were also resolved in an atmosphere of friendly negotiation. Both bodies frequently concerned themselves with self motivation, and at times questioned the extent of their respective mandates. There were times when it appeared that there may have been a duplication of responsibility. Most, but not all the difficulties encountered, were resolved.

beaucoup d'imagination et de ressources. Les directeurs du programme ont mis au point et fait publier annuellement un calendrier des travaux, après approbation par la haute direction. Ce calendrier englobait les divers éléments du programme, ordonnés selon leur nature, et décrivait les réalisations prévues et effectives de chaque facette du programme.

En 1977, le programme CANUSA était très diffus, ses éléments étant répartis dans les deux services parrains, dans les programmes des États et des provinces, dans les universités et dans le secteur privé. Pour faire le point de l'état actuel des techniques, les deux directeurs du programme se sont donné comme première mission de faire l'inventaire détaillé de la recherche sur les tordeuses. Cet inventaire, dont la justesse ne dépendait que de celle des renseignements qui ont servi à le dresser, s'est poursuivi durant tout le programme. Il a servi d'étalon des progrès réalisés et de canevas pour le catalogage des nouvelles études. Il est intéressant de mentionner qu'on a relevé des études qui avaient été omises dans le programme en cours jusqu'à la publication de l'inventaire final. Durant le programme, certains ont affirmé que la publication des inventaires a consommé peut-être davantage que nous oserions l'admettre de cellulose de sapin et d'épinette que les tordeuses mêmes!

Le Conseil mixte du programme et des politiques (CMPP) et le Groupe mixte de planification (GMP) ont agi pour la durée de l'entente en tant que maîtres d'oeuvre de la politique et du programme scientifique, respectivement. Chacun était constitué de 8 membres, 4 de chaque pays. Chacun s'est réuni de son côté au moins une fois par année et, durant la dernière partie du programme, ils se sont rencontrés. Certains ont prétendu que le programme était suradministré, mais il est avéré que la détermination des questions de politique par le CMPP et les critiques de programme par le GMP ont grandement été facilitées par leurs actions concertées.

Chaque année, les réalisations ont été examinées, confrontées au calendrier des travaux et comptabilisées. Les directeurs du programme, en collaboration avec leurs gestionnaires, assemblaient la documentation et planifiaient les travaux et le budget de l'année à venir. Le GMP était chargé d'étudier les documents et de porter à l'attention du CMPP les points forts et les points faibles de la planification et de l'exécution. Les questions délicates telles que la protection de l'environnement et de la santé de l'homme, les répercussions sur les politiques de chaque pays et les questions de publicité et de relations publiques ont aussi été traitées dans une atmosphère de négociations amicales. Les deux groupes se sont souvent préoccupés de la motivation et, parfois, se sont interrogés sur l'étendue de leurs

Late in the Program the JPU authorized an independent review and critique that was aimed specifically at the mandate, functioning, and composition of these two bodies. It is interesting that although the evaluation team addressed the concept of over-administration and did indeed recommend a change, the alternative that was proposed did not differ greatly from the one in existence. Contrary to the criticisms of some, the two governing bodies worked very hard to ensure that the intent of the Program remained intact. Several important administrative and program difficulties were resolved through their efforts. Both served to tie together an extensive and complicated structure and plan into a functioning program. Because each member was closely tied to the fiscal and/or decision-making process, the mix of the administration groups certainly made the tasks of the Program Leaders and Program Managers much easier to complete.

Program Development and Program Cohesion

The Program was developed, coordinated, and implemented through the activities of the two Program Leaders in Washington and Ottawa. Although some of the program personnel changed during the life of the agreement, the Program Leaders Mel McKnight and Chuck Buckner have remained in place from beginning to end. There were some thoughts, at least on the Canadian side, that Program Leadership should rotate, but this idea was abandoned early in the Program to retain the advantage of continuity. This was probably a wise choice, because the two leaders developed program direction and philosophy, diplomatically steered around some major pitfalls, and generally carried their Program when odds would have said it was "dead in the water." Besides which, we still have two broad shoulders upon which to heap all the blame for shortfalls!

The ink was barely dry on the agreement document when the two Program Leaders met to plan program and strategy. Highest on the list of priorities was the draft of a planning document in which to slot all the problems and requirements. Prior to the agreement, the USA fabricated the famous (or infamous, depending upon your preferences) Denver Document, which served as a crude model for what was to come. The International Program was spawned, however, by two meetings that many of you attending this meeting participated in: the first in December of 1977 in Portland, Oregon produced the Portland Papers; the second in January 1978 in Montreal, Quebec contributed the Montreal Manifesto. From those two meetings, the Program Leaders secreted themselves in Orono, Maine, in February 1978, to thrash out the first activity schedule — the Orono ORACLES. How befitting that on

mandats respectifs. Il est parfois apparu que les responsabilités se chevauchaient. La plupart des difficultés, mais non toutes, ont été aplanies.

Vers la fin, le GMP a autorisé l'évaluation indépendante et précise du mandat, du fonctionnement et de la composition du Conseil et de lui-même. Il est intéressant de noter que, même si les évaluateurs se sont penchés sur la suradministration et recommandé des correctifs, la solution qu'ils ont proposée ne différait pas beaucoup du mécanisme en place. Contrairement à ce que certains ont pu prétendre, les deux groupes se sont efforcés de conserver intacte la portée du programme. Grâce à leurs efforts, plusieurs grandes difficultés d'administration et d'exécution ont été surmontées, une structure et un plan complexes et vastes se sont édifiés en un programme opérationnel. Comme chaque membre participait étroitement à la prise de décisions ou au processus financier, le dosage de groupes administratifs a certainement facilité le travail des directeurs et des gestionnaires du programme.

Élaboration et cohésion du programme

L'élaboration, la coordination et l'exécution du programme se sont faites par les deux directeurs du programme à Washington et à Ottawa. Malgré le roulement du personnel, les directeurs Mel McKnight et Chuck Buckner sont restés sur la brèche du début à la fin. Au Canada, on avait envisagé la rotation des directeurs du programme, mais cette idée a été abandonnée très tôt, au profit des avantages de la continuité. Ce choix a probablement été sage parce que les deux directeurs ont imprimé au programme une marque et une doctrine, ils ont évité de façon diplomatique certains écueils dangereux et dirigé leur barque lorsqu'elle semblait irrémédiablement perdue. En outre, comme ils ont bon dos, c'est eux que nous pouvons encore blâmer si quelque chose ne va pas!

L'accord était à peine signé qu'ils se sont rencontrés pour planifier le programme et sa stratégie. En tête des priorités se trouvait la rédaction d'un document de planification où il serait tenu compte, dans leur contexte, de tous les problèmes et de tous les besoins. Avant la signature de l'entente, les Américains avaient rédigé ou concocté, comme vous le voudrez, le document de Denver, modèle brut de ce qui nous était promis. Cependant, le programme international a été l'aboutissement de deux réunions à laquelle beaucoup d'entre vous avez participé: la première en décembre 1977, à Portland dans l'Oregon, qui a donné lieu aux documents de Portland; la seconde, en janvier 1978, à Montréal, qui a abouti au manifeste de Montréal. Suite à ces deux réunions, les directeurs du programme se sont retirés à Orono, dans le Maine, en février 1978 pour produire le premier calendrier des travaux, les

Tuesday night we will all return to the scene of the crime and gorge ourselves on lobsters and other delectable Maine goodies. And so we come the full circle.

On the Canadian side, we took the opportunity of the International Program to put our own house in order by commissioning a task force to review our program and to recommend changes in keeping with the new priorities. It is befitting that the leader of the task force, Chris Sanders from the Great Lakes Forest Research Centre, is here in capacity of co-chairman of the Symposium Program along with Ron Stark, his Portland, Oregon confrere. Using the Task Force report as the guide, we reshaped the CFS program to conform to the aims and objectives of the international agreement. This, say many of our scientists, was the CFS response to the annual $4 million plus contribution from the USA!

The Program relied heavily upon working groups to effect scientific interchange, to coordinate research projects, and to identify gaps in knowledge. Many of the scientists in this assembly participated regularly in working group activities. Initially Program management structured working group meetings formally, but as the Program matured, members of the groups themselves gathered to discuss their natural problems as opportunities were presented. These working relationships, both formal and spontaneous, and formed as a necessity of the CANUSA Program, are a legacy we hope will persist long beyond any research agreement between our two countries. Subject matter concerns are the building blocks of research, and we can be proud of the working groups that the Program generated to address the many problem areas that the overview program was concerned with. As one looks at the current Program outputs: the proceedings of workshops, the symposia, the individual publications, and the many joint publications, one cannot help but acknowledge that the Program has stimulated an atmosphere of joint research and development. If we can be assured that the working relationships developed during the CANUSA Program survive beyond 1984, the time, investment, and dedication of all concerned will have been well worth the investment.

The Program Leaders devised a number of mechanisms for information flow and coordination of the program elements. To facilitate dissemination of Program information, a bi-monthly Newsletter was published. This contained articles on parts of the Program; reviews of subject areas; information on past, present, and future events of interest to program participants; information on personnel; lists of published material; press clippings; and all those other bits of information essential to the cohesion of the Program. The Newsletter has been published in both English and French and has a mailing list of over 2000 in North America and overseas. We owe Janet Searcy, Information Coordinator in the Washington Office, and Jim Mullins, English

ORACLES d'Orono. Combien il est juste et approprié que, mardi soir, nous revenions sur les lieux du «crime» pour savourer du homard et d'autres spécialités délectables du Maine. Ainsi le cercle est bouclé.

Au Canada, nous avons saisi l'occasion fournie par le programme international afin de faire notre propre ménage en créant un groupe de travail pour examiner notre programme et recommander des modifications, conformément aux nouvelles priorités. Il convient que le chef du groupe de travail, Chris Sanders, du Centre de recherches forestières des Grands lacs, copréside le programme du Colloque avec Ron Stark, son confrère de Portland (Oregon). En nous guidant sur le rapport du groupe de travail, nous avons refaçonné le programme du SCF pour le conformer aux buts et aux objectifs de l'entente internationale. Ceci, au dire de beaucoup de nos scientifiques, était la réponse du SCF à la contribution annuelle de plus de 4 millions de dollars des États-Unis!

Le programme reposait énormément sur les groupes de travail pour les échanges scientifiques, la coordination des projets de recherche et la détermination des lacunes dans nos connaissances. Beaucoup des scientifiques ici présents ont participé régulièrement aux travaux des groupes de travail. Au début, il avait été prévu que ces groupes de travail se réunissent officiellement, mais, à mesure que le programme prenait de la maturité, leurs membres ont choisi de se rencontrer dès que l'occasion s'en présentait, pour discuter de leurs problèmes communs. Ces relations de travail, officieuses, spontanées, fruit de la nécessité imposée par le programme CANUSA, sont un héritage que nous souhaitons voir se conserver très au-delà de la durée de toute entente de recherche entre nos deux pays. Les préoccupations disciplinaires sont les pierres d'assise de la recherche, et nous pouvons être fiers des groupes de travail que le programme a suscités pour s'attaquer aux nombreux problèmes dont on avait fait le survol. Devant les réalisations du programme (comptes rendus d'ateliers, colloques, publications particulières, nombreuses publications en collaboration), on ne peut s'empêcher de reconnaître que le programme a favorisé une atmosphère de collaboration dans la recherche et le développement. Si nous pouvions être assurés que les relations de travail instituées durant le programme dureront au-delà de 1984, le temps, l'argent et la motivation de tous ceux qui ont participé auront bien valu la peine.

Les directeurs du programme ont conçu un certain nombre de mécanismes pour diffuser l'information et coordonner les éléments du programme. Dans le premier cas, ils ont créé un bulletin bimestriel, qui réunissait des articles sur des éléments du programme; l'examen des sujets-vedettes; des renseignements sur les événements passés, présents et à venir qui pouvaient intéresser les participants au programme; de l'information sur le personnel; des bibliographies; des

editor with CFS headquarters, debts of gratitude for their untiring efforts in seeing that each Newsletter issue was edited and produced. Both are here to see that the Proceedings of this Symposium are published with the same high standards as are the other CANUSA publications. Here as well, is Joan Murphy, seconded from the Laurentian Forest Research Centre to act as associate editor for the Proceedings of this meeting. In fact the entire CANUSA editorial staff is here, including Martha Brookes from the Corvallis, Oregon establishment, to assist the authors of the symposium in finalizing their presentations in order to minimize delays in the final publication. Other program communications are: the Inventory, mentioned previously (updated twice yearly); the International Directory published annually; the Activity Schedule revised annually; and the annual plans of work and budgets.

The Program

Most of you are aware that the Program was divided into six major target areas: budworm populations and damage evaluations; stand dynamics; economic impacts; treatment strategies; environmental impacts; and pest/resource management systems. Activities in these areas were focused on the mandate of the Program — to deliver to the resource manager improved budworm management systems that were economically viable and ecologically acceptable. Over the term of the CANUSA agreement, more than two thousand research projects and publications have been produced, all identified with specific projects or studies within the activity schedule or study plan. Most of these have been integrated into existing or new management strategies, and CANUSA-sponsored workshops and symposia have delivered new or improved technology to the practitioner. In the initial planning stages of the Program, the Program Leaders and research managers obtained the input of the resource managers that the Program was to serve. During the course of the Program, practicing foresters were involved in the planning and in many instances, in the conducting of research and development activities. In short, we attempted to fabricate a network of iterative research and development, starting and ending with the user, so that program developments would flow easily from the research bench to forest managers.

Beyond CANUSA

Only with time will we be able to appreciate the full impact of the CANUSA Program. Certainly at this point, we are assured that the body of scientific knowledge of the budworms is richer because of it. A number of new applied research projects are also in the hands of the

coupures de presse; et tous les autres éléments d'information essentiels à la cohésion du programme. Le bulletin était publié en anglais et en français, et sa liste de distribution comprenait plus de 2 000 noms, en Amérique du Nord et à l'étranger. Nous sommes fortement relevables à Janet Searcy, coordonnatrice de l'information au bureau de Washington et à Jim Mullins, rédacteur anglophone à l'administration centrale du SCF, pour leurs efforts inlassables dans la révision et la production de chaque numéro du bulletin. Tous les deux sont présents pour faire en sorte que le compte rendu du colloque soit publié selon les mêmes normes de qualité que les autres publications CANUSA. Je nommerai aussi Joan Murphy, détachée du Centre de recherches forestières des Laurentides en tant que rédactrice adjointe. En fait, tout le personnel de la rédaction du programme CANUSA est ici, y compris Martha Brookes de Corvallis (Oregon), pour aider les auteurs des communications à mettre ces dernières dans leur forme finale, dans les plus brefs délais avant la publication finale. Dans les autres communications instituées en vertu du programme mentionnons l'inventaire, dont j'ai parlé un peu plus tôt et qui est mis à jour deux fois par année; l'annuaire international, annuel; le calendrier des travaux, mis à jour chaque année; et les budgets et les plans de travail annuels.

Le programme

La plupart d'entre vous savent que le programme a été subdivisé en 6 domaines principaux: évaluation des populations et des dégâts des tordeuses; dynamique des peuplements; répercussions économiques; stratégies de traitement; incidences environnementales; et systèmes d'aménagement des ressources et de lutte contre les ravageurs. Dans ces domaines, les travaux étaient orientés selon le mandat du programme: mettre entre les mains des aménagistes des systèmes améliorés de lutte contre les tordeuses, économiquement viables et écologiquement acceptables. Pendant la durée de l'entente CANUSA, plus de 2 000 travaux et publications de recherche ont été réalisés, tous identifiés à des projets ou à des études précises figurant dans le calendrier des travaux ou le plan d'étude. La plupart ont déjà été mis en pratique dans des stratégies d'aménagement, anciennes ou nouvelles; par ailleurs les ateliers et colloques parrainés par CANUSA ont permis de confier aux praticiens des techniques nouvelles ou améliorées. Au début de la planification du programme, les directeurs et les responsables de la recherche ont fait appel aux aménagistes auxquels étaient destinés les fruits du programme. Durant l'exécution de ce dernier, les forestiers ont participé à la planification et, dans beaucoup de cas, à la recherche et au développement. Bref, nous avons tenté de créer un réseau de

Program "customers." And the host of studies completed and in various stages of reporting or technology transfer guarantee useful products for the user.

But, as I said in the beginning, the budworm problem is still with us. What we must ensure, is the continuation of the cooperative spirit of CANUSA. Many of the working groups, including those initiated by Program management and those that generated spontaneously because of Program associations, seem destined to continue. A formal but far less structured international management system is in process of evolving. And most of all, the many cross country and cross border contacts generated by the Program seem assured of continuing. So, as we end the CANUSA Spruce Budworms Program, the largest forestry international R & D program ever attempted, I urge all participants to cement the magnificent working relationships and continue them to address the spruce budworms and other forest pest problems of mutual concern in an integrated, cooperative and cost-shared program. Long live the SPIRIT of CANUSA.

R.D. itératif, pour et par l'utilisateur, de sorte que l'acquis de la recherche serait facilement communiqué aux aménagistes.

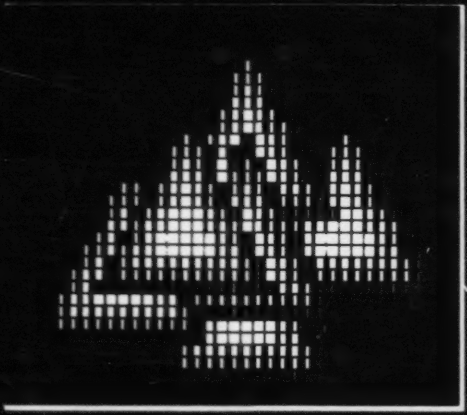
Au-delà de CANUSA

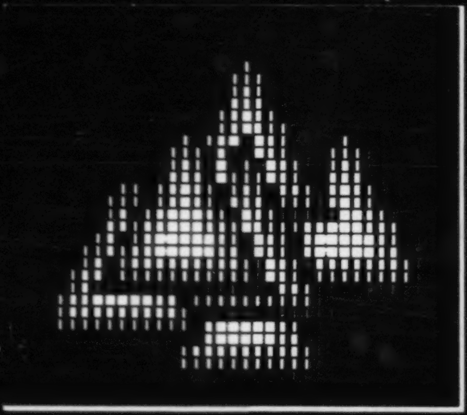
Ce n'est qu'avec le temps que nous pourrons apprécier le retentissement du programme CANUSA. Actuellement, nous sommes déjà assurés que la masse de connaissances scientifiques sur les tordeuses s'est enrichie à cause du programme. Un certain nombre de nouveaux projets de recherche appliquée sont aussi confiés aux «clients» du programme. La gamme des études réalisées ou plus ou moins avancées ainsi que les échanges de connaissances techniques sont d'autres produits utiles, assurés pour les utilisateurs.

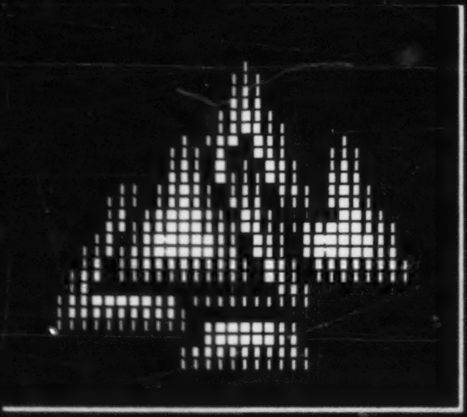
Comme je l'ai dit au début, le problème des tordeuses nous hante encore. Nous devons faire en sorte que l'esprit de collaboration instauré par le programme CANUSA ne meure pas avec lui. Beaucoup de groupes de travail, y compris ceux qui ont été institués par les responsables du programme et ceux qui ont spontanément vu le jour grâce aux associations découlant du programme semblent destinés à durer. Un mécanisme international d'aménagement, officiel et beaucoup moins structuré, est en voie de naître. Plus important encore, de nombreux contacts nationaux et internationaux instaurés grâce au programme semblent assurés de se maintenir. C'est pourquoi, au crépuscule du programme CANUSA, le plus vaste programme international de recherche et de développement en foresterie jamais lancé, j'incite tous les participants à cimenter les incomparables relations de travail qui sont établies et à les cultiver pour résoudre les problèmes causés par les tordeuses et d'autres ravageurs forestiers d'intérêt mutuel, selon un programme intégré, de collaboration et à frais partagés. Vive l'esprit de CANUSA!

Part I

Spruce Budworms – Biology, Ecology, and Population Dynamics







The Taxonomy of the Coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): A Review

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The Genus *Choristoneura* includes 8 species and 4 subspecies that feed on foliage and cones of conifers in North America. Two of them, *C. fumiferana* and *C. occidentalis*, are of major economic importance and erupt in periodic outbreaks that cause severe damage or death to large forest areas. The group is characterized by numerous polymorphisms and by extensive overlap of characters between species. Consequently, identification of individual insects of most species is almost impossible in all developmental stages. Nevertheless, field observations attest to the biological reality of most of the taxa.

The history and taxonomy of the group is reviewed along with various kinds of supporting information based on field and laboratory studies of biology, physiology, behavior, etc. Although some changes in taxonomic status may be warranted, none is recommended at this time. Present distributions of all taxa are mapped and areas of ignorance, uncertainty or sympatry are pointed out. Mechanisms for maintenance of genetic separation are poorly understood for most of the taxa.

Le genre *Choristoneura* comprend 8 espèces et 4 sous-espèces qui se nourrissent aux dépens du feuillage et des cônes des conifères de l'Amérique du Nord. Deux sont d'importance économique : *C. fumiferana* et *C. occidentalis* infestent périodiquement de vastes superficies forestières où elles provoquent des dommages ou une mortalité considérables. Le groupe se caractérise par un polymorphisme diversifié et par de nombreux caractères communs aux espèces, qui rendent l'identification définitive des insectes de la plupart des espèces presque impossible à tous les stades de leur croissance. Néanmoins, les observations sur le terrain démontrent clairement la réalité biologique de la plupart des taxons.

L'historique et la taxonomie du groupe sont abordés avec, à l'appui, divers renseignements tirés d'études, sur le terrain et en laboratoire, de la biologie, de la physiologie, du comportement, etc., de l'insecte. Même si certains réaménagements taxonomiques sont indiqués, aucun ne semble actuellement nécessaire. La répartition actuelle de tous les taxons est cartographiée, et les zones grises, dues au manque de données, à leur incertitude ou aux recouvrements sympatriques, sont signalées. Pour la plupart des taxons, on connaît mal les mécanismes qui maintiennent la ségrégation génétique.

Introduction

The spruce budworm was formally named "*fumiferana*" in 1865 by Clemens who assigned it to the Genus *Tortrix*, based on specimens collected in Virginia (Clemens 1865). Some four years later Robinson used the name *Tortrix nigridia* for what was found to be the same species and *nigridia* became a synonym of *fumiferana*. Soon after Clemens named the spruce budworm from Virginia, other conifer-feeding insects were collected and named in California: *retiniana* by Walsingham (1879), *lambertiana* by Busck (1915) and *carnana* (Barnes and Busck 1920). Further problems and changes in assignment have occurred frequently since that time and several new entities have been named.

Widespread and damaging outbreaks are a principal characteristic of the spruce budworms. Major control actions have been mounted against several of the species, including *fumiferana*, *occidentalis*, *pinus* and *retiniana*, but are not discussed in this review. Historical reports of extensive outbreaks of *C. fumiferana* in New England in 1807 and again in 1890 were mentioned by Freeman (1953). Spruce budworm were also numerous in Ohio and Pennsylvania at that time, although these areas are now beyond the accepted range of this species. Further evidence of the history of spruce budworm outbreaks came from studies of tree rings from several locations in eastern Canada (Blais 1965). Blais found evidence of suppressed growth dating back some 300 years that strongly resembled effects caused by the spruce budworm today. The frequency, extent and severity of budworm outbreaks in eastern Canada appears to be increasing (Blais 1983a). In the western United States, Johnson and Denton (1975) assembled early records of budworm outbreaks in that area and adjoining parts of Canada, and showed that serious outbreaks have occurred there from as early as 1907. The insect responsible for these outbreaks is now known as *C. occidentalis*. Other closely-related species are now recognized that periodically cause serious damage to various spruce-fir and pine forests.

These budworms all appear to be native to North America and we must conclude that extensive outbreaks of several of them have been part of the ecology of spruce-fir and pine forests on this continent for centuries. *C. fumiferana* may form an important part of the cycle of growth and renewal in eastern forests (Baskerville 1975). Perhaps the same is true of the western species in the forests they occupy. Gordon (1984) argues that the spruce-fir forests and spruce budworms evolved together, and that these insects are "an essential factor in maintaining spruce in the stands." Now, however, these insects are in direct competition with human needs for wood products. Because of their economic importance we must have a thorough understanding of their biologies and population dynamics. This requires a well founded taxonomy and reliable methods of field identification. These goals have not been reached.

Major and extensive outbreaks in the late 1940s attracted increased attention to these important pests and led to more intensive study of their taxonomy. A brief review of the progressive steps in differentiating and naming the currently recognized species is appropriate here; for a more detailed review see Powell (1980). Taxonomy of Tortricidae is difficult and it was not until studies were made of the morphology of the genitalia that significant advances were made. From such studies, Freeman (1947a,b) reassigned *fumiferana* to the Genus *Choristoneura* Lederer. Some years earlier the form feeding on eastern pines was seen to be biologically distinct (Graham 1935), but it was not formally named as *C. pinus* until 18 years later (Freeman 1953). Between these two eastern species clear differences exist in "wing pattern, ground colour of the forewings, wing expanse, uncus widths, food plant preferences, and time of flight" (Freeman 1953). Larvae of the two species have the same setal patterns but can be differentiated by measurements of the postclypeal index (MacKay 1953; Cox 1953) and color (Harvey and Stehr 1967).

In 1958 Freeman revised the subfamily Archipinae, creating new combinations of several forms, and gathering into the Genus *Choristoneura* Led., a number of western coniferophagous species, including *lambertiana* Busck, *carnana* Barnes and Busck, *retiniana* Walsingham, and related insects that feed on broadleaved trees. In both the 1953 and 1958 papers Freeman referred to the presence of further closely-related but unnamed taxa among the spruce-fir feeding entities in the Cordilleran Region. He commented on the high degree of variability in both wing maculation and color, and speculated as to their possible status. Obraztsov (1962) did a careful study and descriptions of *Choristoneura* in three major museums. Based on this work he redescribed *retiniana* and named two new species and two new subspecies. Powell (1964) studied Tortricine moths in California, adding comparative biology to the traditional skills of the systematist. He studied both field-collected and reared families and gave recognition to host plant preferences, seasonal life history, and distribution in addition to traditional morphological characters. Powell named one new subspecies and created two new combinations.

By this time other western forms, such as the two-year cycle budworm were being accepted as biologically distinct. Following extensive laboratory studies of insects collected from a wide range of localities across Canada and the United States, Freeman (1967) named four new species, *biennis*, *occidentalis*, *orae*, and *viridis*, and a new subspecies *maritima*, the latter a form of *C. pinus* (Table 1). These separations were supported by evidence from comparative biology and population genetics. Stehr (1967) emphasized the need to consider ecological relationships between insect forms and host species in forest regions in order to interpret taxonomic differences. He recognized the important division between the spruce-feeding taxa and the pine-feeding forms. Other evidence from studies of diapause (Harvey 1967) and larval and pupal colors (Harvey and Stehr 1967) were also presented in support of the taxonomic separations. Review of the Acknowledgments of this series of 1967 papers suggests that it was one of the first genuine CANUSA efforts, as cooperators from 9 provinces and 10 states assisted with collection of insects and other information.

Table 1
Checklist of coniferophagous *Choristoneura* species[1]

Species	Synonym(s)	Code[3]
fumiferana (Clem., 1865)	*nigridia* (Rob., 1869)	*fum*
retiniana (Wlsm., 1879)	*lindseyana* Obr., 1962 *viridis* Free., 1967 n. syn. *spaldingiana* Obr., 1962[2]	*ret*
occidentalis Free., 1967		*occ*
carnana (B. and Bsk., 1920)		*car*
carnana californica Powell, 1964		*cal*
biennis Free., 1967		*bie*
orae Free, 1967		*ora*
pinus Free., 1953		*pin*
pinus maritima Free., 1967		*mar*
lambertiana (Bsk., 1915)		*lam*
lambertiana ponderosana Obr., 1962		*pon*
lambertiana subretiniana Obr., 1962		*sub*

[1] From J.R. Powell, 1983.
[2] Powell, J.R. and J. DeBenedictis, 1982.
[3] Abbreviations used in tables.

Powell (1980) conducted an historical review and analysis of nomenclature in the group. His conclusions, including the synonymy of *viridis* with *retiniana*, and other changes were summarized in the most recent checklist (Powell 1983). There are now ten named species and five subspecies (Table 1). Table 1 also lists the three-letter abbreviations of species names used in tables in this paper. However, although some of the presently named entities warrant separation as full species, others do not. Powell (1980) said "names applied to both Abietoideae- and Pinoideae-feeding *Choristoneura* particularly in western North America, are little more than signs posted at irregular intervals on mosaics of different populations." Stock and Castrovillo (1981) concluded an analysis of isozyme frequencies in five of these species by a statement supporting the view of Powell that "definition of some of the *Choristoneura* species as reproductively isolated entities of comparable rank or genetic integrity is, at this point, artificial."

Powell (1964) commented "probably no Tortricid has been so extensively studied as *Choristoneura fumiferana* (Clemens), yet limits of the species and its relationships with closely related and physiologic subspecific and specific entities are not clear." Most of the present species were accepted as biologically different many years before nomeclatural separation was achieved. This delay in naming resulted from the lack of clear morphological differences between different entities and the wide range of variability in all members of the group. Although clear progress had been made before the CANUSA Program focused renewed attention on these problems, Powell's summation was still largely true in 1979. Further progress in understanding the interrelationships among this group of closely related entities has been made in the past 5 years, as will be detailed in what follows. The objective of this paper is to assemble the present understanding of these species and the knowledge and information on which it is based. However, Powell's conclusion that "the limits of the species and their interrelationships are still not fully clear" is still generally true today.

Geographic Distribution and Hosts

The *Choristoneura* species under consideration all feed on species of Pinaceae and are frequently called "coniferophagous" to differentiate them from members of the Genus that feed on broad-leaved species. Stehr (1967) gave a full discussion of the host associations of the group and pointed to the relationships between taxonomic entities and forest regions. None of the species is strictly host-specific, most of them feeding on two or more hosts. However, they form two groups, one associated with spruces, Douglas-fir and true firs (Abietoideae) and the other feeding on pines (Pinoideae) (Tables 2 and 3). This separation is virtually complete; rarely does complete development occur on a host of the other group. The species may be further divided into groups by geography; two, *fumiferana* and *pinus*, occupy forests of the east and central parts of

Table 2
Coniferophagous *Choristoneura* species and their hosts

	Principal hosts	Occasional hosts
I. Abietoideae Feeding		
C. fumiferana	*Picea glauca* *Picea rubens* *Picea mariana* *Abies balsamea*	*Larix laricina* *Picea engelmannii* *Abies lasiocarpa* *Pinus* spp.
C. biennis	*Abies lasiocarpa* *Picea glauca albertiana* *Picea engelmannii*	*Pseudotsuga menziesii glauca*
C. orae	*Picea sitchensis* *Abies amabilis*	
C. occidentalis	*Ps. menziesii* *Abies amabilis* *Abies concolor* *Larix occidentalis* *Abies lasiocarpa*	*Abies grandis* *Picea engelmannii* *Pinus flexilis* *Tsuga heterophylla* *Pinus albiocaulis*
C. carnana	*Pseudotsuga menziesii* *Abies concolor*	*Pseudotsuga macrocarpa*
C.c. californica	*Pseudotsuga menziesii* *Abies concolor*	
C. retiniana	*Abies concolor* *Abies grandis*	*Abies magnifica* *Pseudotsuga menziesii*
II. Pinoideae Feeding		
C. pinus pinus	*Pinus banksiana* *Pinus resinosa*	*Pinus sylvestris* *Pinus strobus* *Pinus contorta*
C.p. maritima	*Pinus rigida* *Pinus virginiana* *Pinus pungens*	
C. lambertiana	*Pinus lambertiana* *Pinus contorta*	
C.l. subretiniana	*Pinus contorta*	*Abies magnifica* *Pinus jeffreyi* *Pinus washoensis*
C.l. ponderosana	*Pinus ponderosana*	
C. lambertiana (uncertain status)	*Pinus contorta* *Pinus flexilis*	

Table 3
Names and common names of hosts of *Choristoneura* species

	Common name(s)
Abies amabilis (Dougl.) Forbes	Amabilis fir, Pacific silver fir
balsamea (L.) Mill.	Balsam fir
concolor (Gord. & Glend.) Lindl.	White fir
grandis (Dougl.) Lindl.	Grand fir
lasiocarpa (Hook.) Nutt.	Subalpine fir
magnifica var. *shastensis* Lemm.	Shasta fir
Larix laricina (Du Roi) K. Koch	Eastern larch
occidentalis Nutt.	Western larch, western tamarack
Picea engelmannii Parry	Engelmann spruce, mountain spruce
glauca (Moench) Voss	White spruce
glauca var. *albertiana* (S. Brown) Sarg.	Western white spruce
mariana (Mill.) B.S.P.	Black spruce
rubens Sarg.	Red spruce
sitchensis (Bong.) Carr.	Sitka spruce
Pinus albicaulis Engelm.	Whitebark pine
banksiana Lamb.	Jack pine
contorta Dougl.	Lodgepole pine
flexilis James	Limber pine
jeffreyi Grev. & Balf.	Jeffrey pine
lambertiana Doug.	Sugar pine
ponderosa Laws.	Ponderosa pine
pungens Lamb.	Table-mountain pine
resinosa Ait.	Red pine
rigida Mill.	Pitch pine
strobus L.	White pine
sylvestris L.	Scotch pine
virginiana Mill.	Virginia pine
washoensis Mason & Stockwell	Washoe pine
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir
menziesii var. *glauca* (Beissn.) Franco	Rocky mountain Douglas-fir
macrocarpa (Vasey) Mayr.	Big cone Douglas-fir
Tsuga heterophylla (Raf.) Sarg.	Western hemlock

the continent whereas the remaining species are found only in the western Cordilleran regions. Most of the species occur throughout the major part of the range of their principal host species, so the latter must be considered in any review of the insect distributions.

Although there are continuing problems with formal taxonomy of these conifer-feeding species, there is a general acceptance of the biological reality of most of the entities presently named. Collections of insects from single locations usually can be readily identified based on biological observations of host, feeding habit, and colors of larvae, pupae, or adults. The recently identified area in Oregon where hybrids of *occidentalis* and *retiniana* have been found (Volney et al. 1984b) represents an exception. Recent information from pheromone trapping has generally supported previously accepted identities. Thus, the present maps have a good level of reliability through most of the ranges of the different species.

The maps and descriptions of distributions that follow represent a synthesis of available information from recent reports (Powell 1980), including CANUSA reports (Powell and DeBenedictis 1982; Shepherd and Dolph 1979) and published papers (Castrovillo 1982; Stock and Castrovillo 1981), as well as some details from unpublished documents of more limited availability, including Annual Reports of the Forest Insect and Disease Survey (Canada) (Canadian Forestry Service 1939-1983) and other references listed for individual species. The limits of the distributions have been approached from a conservative point-of-view and are based on evidence from collections or other observations, but do not include the most recent results of pheromone trapping. Details of insect distributions are based on data collected principally during periods of moderate to high population densities when reporting is intensive because of economic concerns. Low densities of insects can probably be found well outside the areas where outbreaks occur, perhaps to the limits of the ranges of the major hosts (Little 1971). However, in some areas identity and extent of budworm species are not well documented, especially in the northwest, and areas of doubt remain. These will be identified where possible and deserve further attention. Plantations of small areas of hosts outside the documented limits may also harbor the insects.

C. fumiferana

The spruce budworm is the only eastern representative of the Abietoideae-feeding species. It is associated mostly with the Boreal forest, but also with the Great Lakes-St. Lawrence and Acadian forest regions (Rowe 1972) — wherever balsam fir and white spruce are found (Figure 1). It is the most widespread of all the group as it extends from the shores of the Atlantic provinces and states westward to the foothills of the Rocky Mountains in Alberta and northward to the Arctic Circle in the Mackenzie River valley and the Yukon. It is probably the most important economically as it develops periodic outbreaks and causes considerable tree mortality of its two principal hosts, balsam fir and white spruce (Brown 1970; Kettela 1983). It also causes significant damage to black spruce, red spruce, and subalpine fir. Although sometimes considered to be invariably associated with balsam fir, *C. fumiferana* is also found in pure stands of white spruce, particularly in the southern and extreme northwestern parts of its

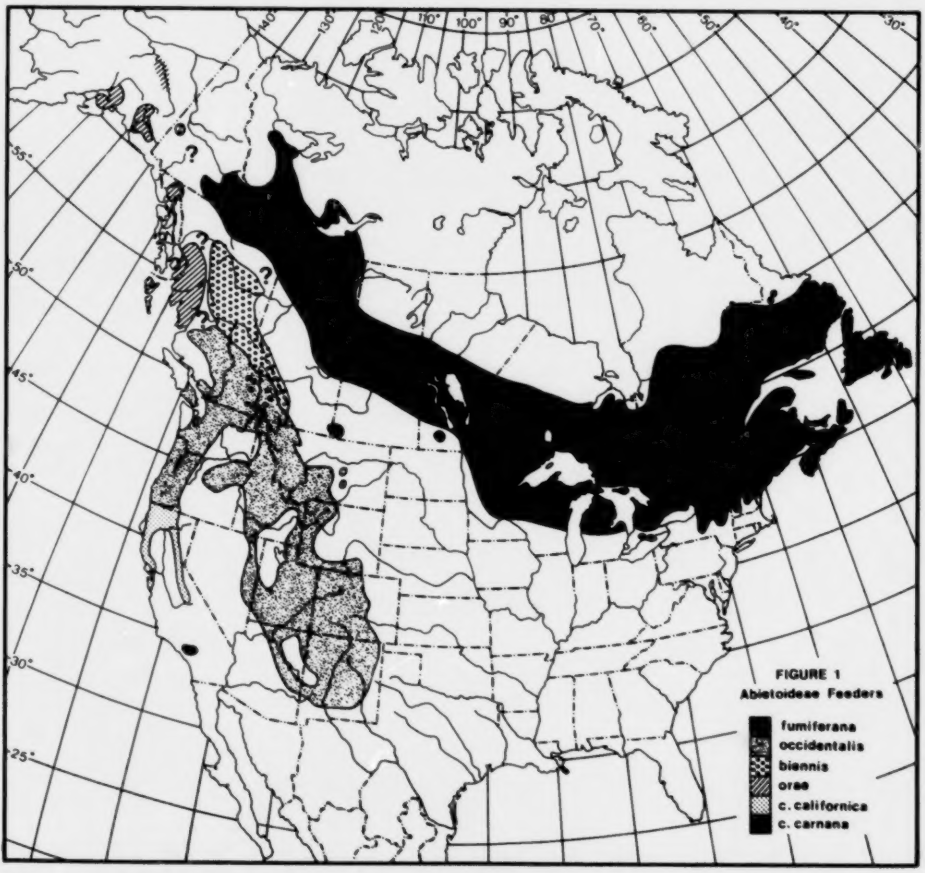


Figure 1. Distributions of *Choristoneura* species in North America: Abietoideae-feeding species.

range. It is known at economically important levels in the boreal forest well beyond the limits of balsam fir, but does not extend as far as the limits of white or black spruce.

Throughout the eastern and central parts of the continent the distribution of *fumiferana* is well documented. Its northern distribution across eastern and central Canada extends almost to the limits of balsam fir. In Quebec the insect is found in all regions where balsam fir is present and indeed can reach outbreak proportions throughout the range of this species in Quebec, including the Upper North Shore (Blais 1983b). Recent small infestations in Labrador (1980) show that the insect can occur to the northern limits of balsam fir in that region. The southern limits of spruce budworm in the eastern and central parts of the continent closely follow the range of the two principal host species. In the Cypress Hills (Alberta/Saskatchewan) and Spruce Woods (Manitoba), *fumiferana* outbreaks have caused considerable damage to isolated forests of white spruce. Farther east across the Lake States, Ontario, New York and New England, the limit of spruce is noticeably south of that of balsam fir. Here also *fumiferana* infestations are found in white spruce with no association of balsam. When the ranges of white spruce and balsam fir extended further south in the Appalachian Range before human disturbance (Gordon 1984), it is probable that spruce budworm were there, as the type specimen collected in Virginia about 1865 was some 600 km (380 mi.) southwest of the nearest present population.

The western and northwestern limits of *fumiferana* are not well documented. Much of this area is remote, partly mountainous and of very difficult access. Infestations have been recorded in much of northwestern Alberta and northeastern British Columbia as well as in the southern part of the Northwest Territories and Yukon (Unger 1974, 1983). Much of this area is beyond the range of *A. balsamea*, so some of the infested areas, such as those along the MacKenzie River are in pure spruce stands. A serious outbreak in this area from 1957-1975 produced mainly top-kill and led to "club-top" trees, but caused very little mortality. Although host species are common in the Upper and Lower Foothills regions of the Boreal forest (Rowe 1972, 19a, 19c) and in the East Slope Rockies region (Subalpine region SA.1) along the Alberta/British Columbia border, there are no authenticated records of *fumiferana* from these areas. *Biennis* is known from higher altitudes in the western parts of the Region SA.2 but no spruce budworm appear to be present in most of this area. Elsewhere in northeastern British Columbia budworm occur in subalpine fir mixed with white or Engelmann spruce. Collections, identified as *fumiferana*, have been recovered from both of these western hosts (Freeman 1967). It has also been found in the Yukon (Freeman 1967) and may be part of the "complex" in the area of Fairbanks, Alaska (E.H. Holsten, personal communication). In this region *fumiferana* may be sympatric with *biennis* or *orae*. The difficulties of differentiation among these entities make accurate definition of the western limits of *fumiferana* impossible at this time.

C. pinus pinus

The jack pine budworm feeds principally on jack pine, but it also attacks Scots pine and has been recovered from other hosts (Table 2). Significant outbreaks have been recorded in the Lake States (Batzer and Millers 1970) and adjoining provinces as well as in Manitoba and Saskatchewan (DeBoo and Hildahl 1968; Brandt and McDowall 1968), particularly in pine plantations. Damage includes defoliation, reduction in male and female cones, growth reduction, top killing, and mortality (Batzer and Millers 1970; DeBoo and Hildahl 1968). Mortality following severe outbreaks in the Lake States can reach one third of the merchantable volume (Clancy et al. 1980).

Although Freeman (1953) reported *C. pinus* from Nova Scotia other reports indicate that it was not found east of Ontario (Brown and MacKay 1943; Prentice 1966). However, Webb and Bean (1967) report its presence over the southern range of jack pine in Canada, which implies its presence in New Brunswick and Nova Scotia. The first recent record in Quebec was near the Ontario border in 1967 (Canadian Forestry Service 1939-1983). It appeared to spread steadily eastward because Benoit and Martineau (1973) reported low numbers over a considerable area of Quebec. Collections in 1971 near Dunphy, New Brunswick were listed as new records (Canadian Forestry Service 1939-1983), but in the decade following numerous collections were made throughout most of New Brunswick and in adjoining parts of Nova Scotia. Although evidence for its earlier occurrence in eastern Quebec and the Maritimes is scanty, its presence through most of the eastern range of jack pine now appears to be established. This host is also present in Maine and Brower (1983) reported small numbers of jack pine budworm at light traps in 12 localities during the past 20 years. However, it was not reported by the Northeast Forest Experiment Station from 1961-1974 and tree damage has not been reported. The distribution map (Figure 2) is based on maps of Batzer and Millers (1970), Brandt and McDowall (1968), DeBoo and Hildahl (1968) and Prentice (1966), and includes recent records from Quebec and the Maritimes.

The western limits of *pinus* appear to coincide closely with the Alberta-Saskatchewan border. It has been recorded in southwestern Saskatchewan in the Cypress Hills which straddle the border (Canadian Forestry Service 1939-1983). There are no recent reports of *pinus* west of the Saskatchewan border, although the range of its host extends to the northern half of Alberta.

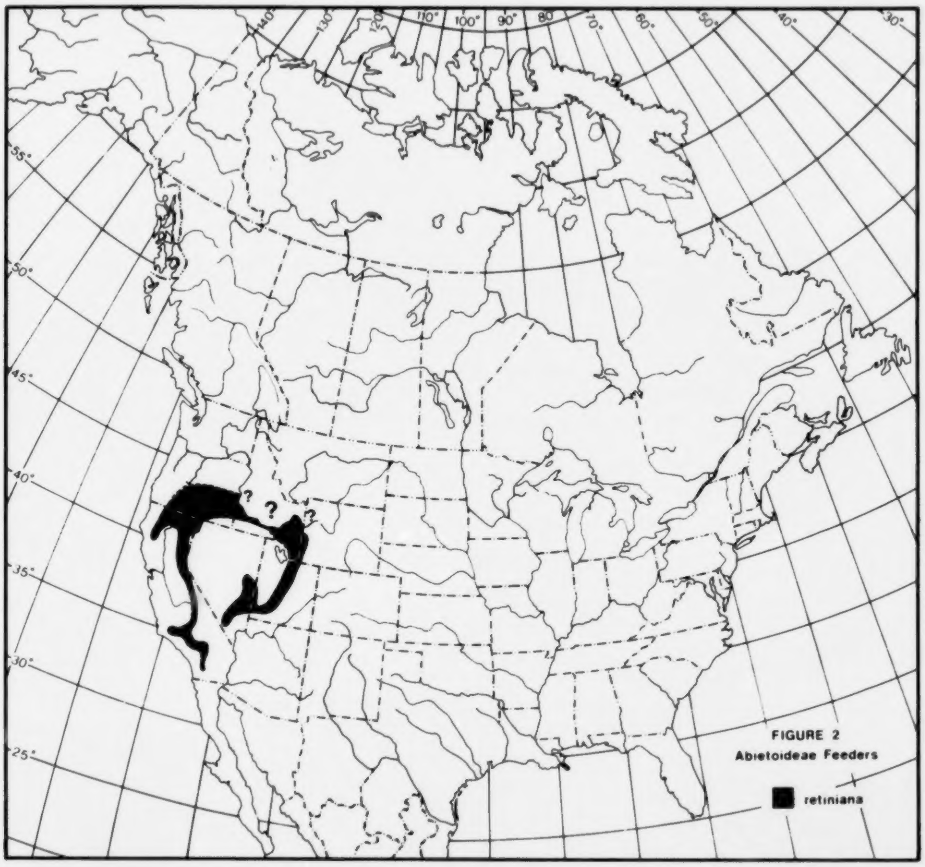


Figure 2. Distribution of *Choristoneura* species in North America: *Choristoneura retiniana*.

Two early reports of *pinus* in the region, one at Field, British Columbia (Prentice 1966) and the other from *P. contorta* in the foothills of Rocky Mountains near Coleman, Alberta (Canadian Forestry Service 1967) are more probably *lambertiana* which is known from the southern foothills area on *P. flexilis* and *P. contorta*. A recent report of *pinus* from jack pine plantations in Nebraska (James 1979) has been confirmed as *C. pinus* (P.T. Dang, personal communication) rather than *C. lambertiana* whose natural distribution is closer. This apparent large extension of distribution probably represents a transfer on planting stock which came from Minnesota (James 1979).

C. pinus maritima

This subspecies of *C. pinus* was named by Freeman (1967) on the basis of 24 adults collected from *P. virginiana* and *P. rigida* at isolated locations from Barnstable, Massachusetts to Morehead, Kentucky. Other records are very sparse. Castrovillo (1982) shows its distribution as extending in a broad band along the higher elevations of the Appalachian mountains. Dang (personal communication) reports collections of *maritima* from near Halifax, Nova Scotia, and specimens resembling *maritima* in collections from Nova Scotia, Michigan and Manitoba. Thus, *maritima*, if a valid subspecies, may be sympatric with *pinus* in the southeastern limits of the latter. Although life history and feeding behavior resemble those of *pinus*, populations are generally low and not known to fluctuate widely. Widespread infestations or significant tree damage have not been recorded. Further study of *maritima* and its relationship to *pinus* are needed.

C. occidentalis

Budworms found in the western parts of Canada and the United States may also be grouped according to host. Of the species that feed principally on firs and spruces *C. occidentalis* Free. is the most widespread and of the greatest economic importance because of the resultant reduction of radial increment, seed losses, top kill, and mortality (Fellin 1980). This insect was not recognized as a serious threat to coniferous forests in the northern Rockies until 1922 (Fellin et al. 1983). Since that time there have been several major outbreaks. The history, extent, and damage caused by these outbreaks have been reported, both for the United States (Johnson and Denton 1975; Shepherd and Dolph 1979) and for Canada (Harris et al. 1985). For much of this time *C. occidentalis* was considered to be the same as the *fumiferana* of eastern forests. However more intensive study showed differences in its biology and morphology that led to its taxonomic separation (Freeman 1967).

C. occidentalis has a wide distribution from southern Arizona and New Mexico to the Fraser Valley of southern British Columbia (Figure 1). Its principal host is Douglas-fir but several species of *Abies, Tsuga, Larix, Picea*, and occasionally *Pinus*, are also suitable and may be subject to heavy attack (Carolin and Honing 1972) (Table 2). Most of its major hosts occupy the same or a less extensive range than Douglas-fir and are present in mixed forests with the latter. This range constitutes principally the Montane forest region in Canada, and its equivalent, the Interior Douglas-fir forest in the United States (Stehr 1967), but also extends to other forest types where Douglas-fir is present, such as the Coast and Subalpine forests of British Columbia and several other forest cover types in the United States (Eyre 1980).

The distribution of *occidentalis* in British Columbia (Figure 1) is based on the map of Shepherd and Dolph (1979). A recent report by Harris et al. (1985) shows a more limited area for this species, but it is based on the presence of defoliation visible from the ground or air, and low populations will be present beyond these limits. Harris et al. (1985) report a collection from Bella Coola, but *orae* is also suspected from this area and differentiation by pheromones was not possible. The northern limits of this species and its relationship to neighboring populations of *orae* and *biennis* are not well understood.

The distribution of *occidentalis* (Figure 1) does not extend much beyond that of Douglas-fir. In western Alberta where the range of Engelmann spruce extends east of that of Douglas-fir, *occidentalis* has not been found. In central British Columbia the range of Douglas-fir and Engelmann spruce terminate at about the same latitude as the limits of the *occidentalis* distribution. Subalpine fir, which is a common host in the southern parts of the *occidentalis* distribution, extends considerably north of the range of Douglas-fir and Engelmann spruce, but does not appear to support populations of *occidentalis*. Thus, although true firs and other species are important hosts of *occidentalis*, its normal distribution does not extend byond the range of its principal host, Douglas-fir.

C. carnana

In the southern portions of the range of Douglas-fir in the Sierra Nevada and Coast Ranges of California, *occidentalis* has not been found. In these areas there are two subspecies of *carnana* which, although formerly considered to be pine-feeding species, are now recognized as part of the complex associated with the Abietoideae (Powell and DeBenedictis 1982). *C. carnana carnana* is found on *Pseudotsuga macrocarpa* (Table 2) in the San Gabriel mountains of southern California — its distribution is limited and its numbers not great (Figure 1). A northern subspecies, *C. carnana californica*, is present in the central Sierra Nevada, southern Cascade range, and the north Coast Ranges of California, where it adjoins *occidentalis* near the Oregon border (Powell and DeBenedictis 1982). Both subspecies are very closely related to the spruce-fir feeding species, particularly *occidentalis*. In fact *C. carnana californica* may represent only the extension of *occidentalis* in California (Powell and DeBenedictis 1982). If this can be established, the nomenclatural priority of *carnana* may necessitate the reduction of *occidentalis* to a synonym.

Collection records for *occidentalis* and *carnana* do not extend to the southern limits of Douglas-fir in Arizona or in Mexico. Extensions of the distribution of *occidentalis* and *carnana* and the presence of closely allied forms may be expected in northern Mexico. DeBenedictis (personal communication) has acquired two specimens of *Choristoneura* collected from *Pseudotsuga* in the Mexican province of Coahuila that closely resemble *carnana*. *C. occidentalis* may indeed be found south of its present limits or it may be replaced by *carnana* in these southern forests.

C. orae

Two additional Abietoideae-feeding budworms are found in central and northern British Columbia and adjacent Alaska. They have been named as separate species although their boundaries with and relationships to both *occidentalis* to the south and *fumiferana* to the north and east are uncertain.

In the coastal forests of Sitka spruce and Pacific silver fir, *C. orae* Free. (Freeman 1967) occurs. It has been found as far south as Ocean Falls, British Columbia and in the Queen Charlotte Islands (Figure 1). Budworm infesting Sitka spruce near Haines, Alaska in 1948 were considered by Stehr (1967) to belong to this species. Similar insects have been collected from the vicinity of Anchorage, Alaska including the Kenai peninsula and from the Copper River Basin (Holsten 1980 and personal communication). The host in these locations is white spruce. Although there are no records of collections from the Alaska panhandle, the populations described probably represent one species (Stehr 1967) that inhabits the entire Coast forest (Rowe 1972). The fir component, Pacific silver fir, which serves as host to *orae* in the southern one-third of its range is not found in the northern parts where Sitka and white spruces are the main hosts. Outbreaks of *orae* are generally short-lived and do not cause serious damage. Control operations planned for the Copper River infestation in 1984 were suspended because populations appeared to collapse (E.H. Holsten, personal communication).

C. biennis

Another Abietoideae-feeding budworm (*C. biennis*), occurs in the interior and higher elevations in British Columbia. The name of this species recognizes its two-year life cycle (Shepherd 1961; Freeman 1967; Harvey 1967). Hosts of *biennis* are subalpine fir and western white spruce (Table 2). The distribution of *biennis* (Figure 1) is based largely on the map of Shepherd and Dolph (1979) with some modifications. Stehr (1967) considered its distribution coincided with the Subalpine forest region (Rowe 1972) and adjacent sections of the Boreal forest to the northeast. However in the south-eastern parts of its distribution, it has been found in the Montane forest region. At lower latitudes populations are confined to the upper altitudes, occasionally in the same areas occupied by *occidentalis*, but separated by some 1500 m (5,000 ft) in altitude. Damage caused by *biennis* may be heavy but its biennial cycle allows the trees to recover in alternate years and reduces its overall impact (McKnight 1968).

The boundaries of the above three species in British Columbia are in some doubt in several areas, as indicated by the question marks on the map (Figure 1). Populations reported in 1983 on white spruce, alpine fir, and western hemlock in the Nass River valley of the Prince Rupert region illustrate some of the problems in this group (Van Sickle and Wood 1983). These populations were first considered to be *biennis* but field evidence of heavy defoliation in several successive years suggests the insects have a one-year cycle (or two overlapping two-year cycles). Early results of 1984 trapping tests using synthetic pheromones in this area suggest that two species are present: *orae* and *occidentalis* or *biennis* (R.F. Shepherd, personal communication). Further trapping tests and other studies are needed to establish the distributions and interrelationships of budworms in much of central and northern British Columbia and adjoining areas to the north and west.

C. retiniana

A fifth Abietoideae-feeding *Choristoneura* has been recognized for some years as the "Modoc" or green budworm from the Warner Mountains in California. The most common host of this species is white fir, but it is also found on grand fir and Douglas-fir (Table 2). This form was given species status by Freeman (1967) and named "*viridis*" because of the body color of the larvae. However, it has now been established that the prior name of *retiniana* Walshingham should be accepted, and "*viridis*" becomes a synonym along with *lindseyana* Obraztsov 1962 (Powell 1983) and with *spaldingiana* Obraztsov 1962 (Powell and DeBenedictis 1982).

Recent studies reported by Powell and DeBenedictis (1982) and Volney et al. (1984) have enlarged the previously known distribution of *retiniana* (Figure 2). It has now been found in the Cascades of Southern Oregon as well as the mountains of California, and the Great Basin and Wasatch Ranges of central Utah and the Schell and Snake Ranges of eastern Nevada. Its northern limits are still not well known; green budworm larvae were described from the Ochoco National Forest, Oregon (MacKay 1962) and from near Burns, Oregon (V.M. Carolin, personal communication). The 1922 record of larvae from *A. grandis* at Priest Lake in northern Idaho (MacKay 1962) appears to be the only one from that state as none were found in southern Idaho or northern Nevada (Powell and DeBenedictis 1982). Although usually associated with white fir, *retiniana* has not been reported from the southeastern range of that host in Colorado, Arizona, or New Mexico. *Retiniana* also feeds on grand fir in the southern range of that host. It has not been reported, however, from large parts of the range of grand fir in northern Oregon, Washington, Idaho (with the exception noted) or British Columbia. Collections from Utah suggest that the distribution of *retiniana* may extend beyond that of the White-Fir forest type (Eyre 1980) as suggested by Stehr (1967).

In the Warner and nearby ranges of northeastern California and adjacent areas of Oregon, outbreaks of *retiniana* occurred during 1959-1962 and 1973-1975 (Ferrell 1980; Dolph 1980). Outbreaks of this species are usually short (3-4 years) and, although they reduce radial growth and may produce as much as 77 percent top kill, they do not cause any long-lasting effects or mortality. Populations are probably sparser and have even less effects on trees in the southern and eastern parts of the range.

Choristoneura n. sp.

A further member of this Genus has been reported in collections of *occidentalis* on Douglas-fir and grand fir in eastern Oregon and Washington (Carolin 1980). Its biology appears similar to that of western spruce budworm, but the larvae may feed before overwintering (V.M. Carolin, personal communication). It pupates about two weeks earlier than the western budworm and the adult is much smaller. It has not been named, nor is more known about its biology and relationships to other *Choristoneura* species, but it appears to belong to the Abietoideae-feeding group.

C. lambertiana
In the west, three forms of *Choristoneura* that feed on Pinoideae are all considered to be subspecies of *C. lambertiana*. Along with the eastern *C. pinus*, they form the *Lambertiana* complex (Powell 1980). All members of the complex tend to be smaller than the Abietoideae-feeding group and have colors dominated by ochreous, red and creamy, or silver, rather than the grays of the latter. Their biology closely resembles that of the spruce-fir feeders but feeding is more frequently, sometimes almost exclusively, on the cones and staminate flowers. Tentative distributions of the three subspecies are shown in Figure 3.

C. l. lambertiana The nominate subspecies has distinct markings. According to Powell and DeBenedictis (1982) it is found only in south-central Oregon and adjacent Siskiyou County, California where it feeds on sugar pine. In other parts of the range of this host in the Sierra Nevada and the Southern Cascades, *lambertiana* is not found.

C. l. subretiniana This distinctly marked subspecies feeds on *P. contorta* as well as *P. jeffreyi* and *P. washoensis* in the Warner Mountains of Oregon and California, in the Sierra Nevada, and in southern California. It is also found on the eastern side of the Cascades in Oregon as far north as Bend and possibly farther (G.E. Daterman, personal communication). Its life history and biology have been described by Stark and Borden (1965) who considered that tree reproduction was not seriously affected even though as many as 90 percent of female cones were infested. Populations appear to remain generally at low levels and economic importance is usually low.

C. l. ponderosana Adults of this subspecies are typically without the pattern of rust or reddish markings common to *lambertiana* and *subretiniana*. Larvae feed on *P. ponderosana* and *P. flexilis*. It is most common on the east slope of the Rocky Mountains in Colorado and western Nebraska (Stevens et al. 1977). Powell and

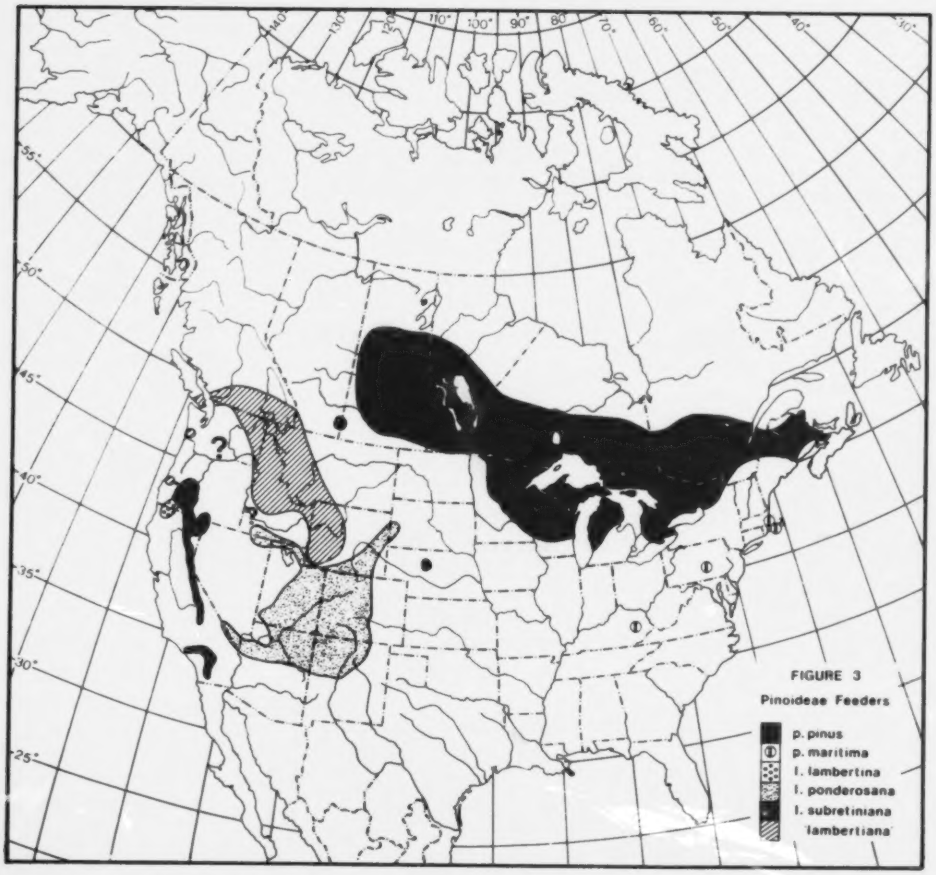


Figure 3. Distributions of *Choristoneura* species in North America: Pinoideae-feeding species.

DeBenedictis (1982) include other more northern populations "of varying atypical phenotype scattered throughout the mountain ranges of northern Arizona, southern Nevada, Utah and northwest" as essentially part of this species. A widespread outbreak was recorded in 1973-1975 over the Rocky Mountain area of the western United States (Stevens et al. 1977). Heavy feeding, shoot destruction, and growth reduction, but little if any mortality were reported. Furthermore, the most severe damage was only in restricted areas and of short duration, thus, the economic importance of the species appears low.

***C. lambertiana* uncertain status (designated "*lambertiana*")** Extensive infestations identified as *C. lambertiana* were reported on *P. contorta* in Idaho and Montana during the 1960s. Although populations of this species may be widespread, and local damage including top kill, may be extensive, the duration of high populations appears short and has never been considered to reach outbreak levels (McGregor 1970). In Canada similar insects were present in moderate numbers during the 1960s on *P. flexilis* and *P. contorta* in the foothills region of southwest Alberta (Canadian Forestry Service 1939-1983). However, there are no records of this insect north of latitude 52° N which suggests it is absent from much of the northern range of these hosts. More recently it has been found in south-central and southeastern British Columbia (T. Gray, personal communication). Figure 3 shows these extensions of the distribution of this species, which is also expected to be found in Washington but probably not the eastern Cascades (V.M. Carolin, personal communication). As shown in Castrovillo (1982), these populations, although considered to be *C. lambertiana*, are of uncertain affiliation and have been designated as "of uncertain status."

Although geographically closer to *ponderosana*, these northern populations from Wyoming to Alberta and British Columbia contain two distinct color morphs — a distinctly marked form resembling *lambertiana* and a form in which banding is reduced, suffused, and indistinct (Stehr 1967). This second morph resembles *ponderosana*, but Powell (1980) considers that populations of the latter "consist entirely of a more extreme washed out phenotype." The collections Stehr (1967) studied, many of which are identified in Harvey and Roden (1979), were considered to be samples from unitary interbreeding populations and, therefore, Stehr concluded the two forms to be components of an intrapopulational polymorphism. This view was supported by breeding results (G. Stehr, unpublished). Of 13 collections from both *P. contorta* and *P. flexilis*, all but four were polymorphic. Four collections from Alberta and Montana contained only the distinctly banded forms; however, mixed collections were received from the same areas. All collections from Colorado, Wyoming, and Oregon contained both morphs. A collection from *P. ponderosana* from Baker, Oregon contained only 7 of 151 adults of the diffuse-patterned form compared to 144 with distinct patterns. Ratios of the two forms were almost equal in all other collections regardless of host and showed no trends (G. Stehr, unpublished).

In the coastal areas of Oregon and Washington, small numbers of a closely related budworm have been found (J.A. DeBenedictis, personal communication). These insects are similar to *lambertiana* and *subretiniana* but are generally more heavily colored and darker. Similar insects have been found recently in the Vancouver area (T. Gray, personal communication). Numbers of these insects are low and although they seem to be a coastal population, their affiliation is uncertain. Preliminary tests indicate the pheromones of insects collected near Vancouver are different from those of "*lambertiana*" (T. Gray, personal communication).

The identity and relationships of all these *lambertiana*-like insects from the north western states and adjacent parts of Canada cannot be resolved without more study. The status of the two morphs of "*lambertiana*" complicates the taxonomy. Powell (1980) felt there was evidence of a "clinical change in phenotype in a broad arc through the northern Rocky Mountain States." Evidence from collections received by Stehr is not fully consistent with this hypothesis. Further difficulty may be caused if there is hybridization where the insects are sympatric with *occidentalis* or *retiniana*. Information is scarce from much of the area and the normally low economic importance of the group dictates little support for the intensity of study needed to unravel the taxonomic problems. However, in spite of the difficulties in the northern areas, there is substantial evidence for the integrity of three subspecies of *C. lambertiana* farther south (Powell and DeBenedictis 1982).

Sympatries

Several areas have been clearly established where two or more coniferophagous *Choristoneura* are sympatric. In other areas some overlap between two species is possible or suspected, and partial sympatry may exist. Powell and DeBenedictis (1982) specifically addressed sympatries in the southwestern United States. Their conclusions and other obvious and suspected sympatries are listed in Table 4. The identity and relationships of the western members of the *Lambertiana* complex are not well enough known to consider possible sympatries within the Pinoideae-feeding species. *C. pinus* appears not to be sympatric with any other members of this group. Thus only the Abietoideae feeders are included in Table 4, although their sympatries with some Pinoideae feeders are included. Question marks on Figures 1 and 3 indicate possible areas of sympatry. In a narrow zone of the northern

Sierra Nevada and in southwestern Utah, three species occur together: *retiniana*, *occidentalis*, and *subretiniana* (Powell and DeBenedictis 1982). More than two species may be sympatric in parts of interior British Columbia. Mechanisms that may act to maintain the integrity of these *Choristoneura* species are discussed below.

Table 4
Known and possible areas of sympatries of coniferophagous *Choristoneura*[1] spp.

Species	Sympatry	Status[2]	Areas of Sympatry
bie	*fum*	P	NE B.C.; Yukon, Alaska
	occ	D	SE B.C. — altitudinal separation?
	ora	P	central B.C.
ora	*occ*	P	Bella Coola?, Kispiox? Nass R.?
	fum	P	Alaska? Yukon?
	bie	P	as above
	lam	P	SW B.C.
fum	*bie*	P	as above
	ora	P	as above
	pin	D	entire range of *pin*
occ	*ora*	P	as above
	bie	P	as above
	ret	D	OR; NV[3]; UT[3]
	'lam'	D'	entire range of *'lam'*
	pon	D	UT; AR
car	*occ*	P	S.OR; N.CA
	ret	D	CA
ret	*occ*	D	as above
	sub	D	NE.CA
	pon	D	NV; UT
	car	D	CA

[1] Lists Abietiodeae feeders only, except where they are sympatric with Piniodeae feeders. See text.
[2] D = demonstrated; P = possible or suspected.
[3] Powell and DeBenedictis, 1982.

Morphological Differences

Early field studies of budworms in both eastern and western forests led to the suspicion that more than a single entity was present and morphological differences were sought on which to base taxonomic separations. The results still do not permit reliable taxonomic identification of individual insects of most of the species, particularly if collection location and host are not known. However, they have provided useful insights into relationships among the members of the group and have uncovered characters that assist identification of some of the species.

Egg Size

Eggs of *Choristoneura* are variable in size and shape, and are laid in clusters that also vary in size. Campbell (1958) reported differences among egg weights of entities now identified as *fumiferana*, *biennis*, and *pinus*. He also reported egg weights of some F1 hybrids to be much larger and others smaller than those of either parent. Harvey (1983c) showed that mean weights of initial eggs (Ei) in *fumiferana* are relatively independent of environmental conditions during development of the parent, but are determined by her genetic constitution. Fecundity is related to Ei and to genetic constitution and nutrition of the female. Further, among *fumiferana* populations, Ei values are correlated with latitude and longitude (Harvey 1983b). Harvey (in preparation) found that Ei values for *lambertiana subretiniana*, *l. ponderosana* and "*lambertiana*" were fully twice those of *pinus*. Differences among the spruce-fir feeders are smaller. These differences lend support to some of the taxonomic separations.

Larvae

Separation and identification of early-instar larvae is usually impossible although host and feeding habit sometimes permit tentative identification. Identification of late-instar larvae is not much more reliable. MacKay (1962) carried out intensive studies of larval collections from many locations of species now known as *fumiferana, orae, occidentalis, retiniana, pinus, maritima*, and "*lambertiana*" (from *P. flexilis* in Yellowstone National Park). She described differences and developed a key based largely on larval color. Even using the key she admitted that "the identification or individual specimens or small groups would be difficult" because of variation among the larvae (MacKay 1962). The postclypeal index which proved useful in separating larvae of *pinus* from *fumiferana* was not helpful in the separation of western populations (MacKay 1962).

Color and patterns of mature larvae were also shown to differ among species (Harvey and Stehr 1967). This information was used to support separation of several of the entities at the specific level. Harvey and Stehr (1967) noted the existence of sex differences in larval colors in most of the species. However, they did not find any diagnostic differences that would permit sure separation of individual larvae of all species.

The limited usefulness of color as a dependable morphological character was recognized in early studies. More recent research has provided direct evidence of genetic and environmental influences on larval color and its variation. Further analysis of larval color scores of *fumiferana* reported by Harvey and Stehr (1967) has demonstrated a cline in percentage of dark prothoracic shields from higher in the east to lower in the northwest (Harvey 1981). Lorimer (1982) found that larval pigmentation frequencies of *fumiferana* differed by host species and between populations. More recently, Volney et al. (1983a) have demonstrated a dependence of larval coloration in *retiniana* and *occidentalis* on temperature, as well as on sex and genetic background. They developed an enlarged coding system for color and pattern of larvae, pupae, and adults of these two species in parts of south-central Oregon where they are sympatric. In spite of environmental effects, this scoring method permitted allocation of individuals to species and lineage with a calculated accuracy, and established the existence of some natural hybridization in the area of study. Several lines of evidence suggest the likelihood of other clines that may add further difficulty to the usefulness of coloration in identification of larvae.

Despite the above difficulties, groups of late-instar larvae from known hosts can be identified with reasonable certainty, although chances of success are better with some species than others. For example, larvae of *pinus* and *retiniana* both have distinguishing colors and can be readily separated from other members of the group. Nevertheless, there is little reason at this time to challenge MacKay's (1962) pessimistic statement that "no practical key to the late-instar larvae of this group can ever be produced."

Pupae

Morphological characters that would allow separation of pupae have not been found either. Campbell (1953) drew attention to the shape differences between *pinus* and *fumiferana*. Similar trends are found in comparisons between other pine-feeding species and those feeding on spruce-fir, but here also there is appreciable variation. Color and pattern of newly moulted pupae are generally different between species (Harvey and Stehr 1967) and support their separation (Freeman 1967). The almost transparent pupal case of *retiniana* is exceptional and is practically uninfluenced by developmental temperatures (pupal ground color and pupal band color — Volney et al. 1983a). Thus it can be useful in identifying individuals of this species. However, pigmentation intensity and pattern are highly variable in all other species and of little assistance in identifications.

Larval and pupal color depends partly on the presence of yellow and blue chromoproteins in the hemolymph (Schmidt and Young 1971). The color is best seen in the wing pads of pupae within 24 hours of pupation (Stehr 1959). Pupal color helps characterize some species (Harvey and Stehr 1967). In all species, except *pinus*, females are polymorphic for hemolymph color, although the ratios vary (Stehr 1959; Harvey and Stehr 1967); in *pinus* all females have yellow hemolymph. It is interesting that in the subspecies *maritima*, females are polymorphic, with yellow-green ratios close to those of *fumiferana*. Males of Abietoideae-feeding species (except for *retiniana*) are also polymorphic for haemolymph color, but males of several Pinoideae-feeding species are monomorphic yellow. Should these ratios prevail for all populations of these species, then hemolymph color could assist in separation of some sympatric species. Thus in an area where *subretiniana* and *retiniana* are sympatric, the male pupae could be differentiated clearly by pupal color: yellow = *subretiniana*; green = *retiniana*. However, this criterion is not useful for females generally, is of little help in many separations, and requires freshly moulted pupae.

Adults

Adult maculation, both color and pattern vary widely within and among the species. Adult descriptions have been reported by Freeman (1953, 1958), Powell (1964), Powell and DeBenedictis (1982), and Volney et al. (1983a). The pine-feeding species generally tend to be more reddish and less polymorphic and the spruce-fir more grayish; males tend to be darker and females somewhat lighter in all species. The high level of variability is also increased by the expression of the "brown-female" character (Stehr 1955) which is present to varying degrees in all species, particularly the spruce-fir feeders (Stehr 1964). The reported "morph" difference in "*lambertiana*" populations further complicates use of colors to distinguish adults to species level. *C. carnana* appears to be monomorphic for adult color (J.A. DeBenedictis, personal communication) which may assist in its separation from neighboring species, but this is an exception as the wide variation in adult color is general through the group.

The physiology of adult color in *occidentalis* and *retiniana* has been shown to be influenced by developmental temperature (Volney et al. 1983a); lower temperatures producing darker or grayer individuals, high temperatures producing lighter or redder individuals. Geographic differences in developmental temperatures may therefore contribute to the wide variation in adult color, both within and among species and the existence of clines in coloration of several species is probable.

Studies of other morphological characters of adults have not proved more successful in providing a morphological basis for separations of these species than maculation. There are, at present, no comprehensive keys to adults or immature forms for this group. Keys to adults were developed by Freeman (1958) and Powell (1964), but both keys are limited geographically in their coverage and do not include all currently named species. Freeman (1967) found no reliable distinguishing character in the male or female genitalia. Although he noted differences in numbers of cornuti on the male aedeagus, the overlap among species limited its use as a reliable specific character. Adults of the pine-feeding species are generally smaller than the spruce-fir-feeding species. However, such differences are of little use because of the extent of intraspecific variation and of the effects of temperature and nutrition during larval development.

The search for morphological characters that will permit unambiguous separation of budworm species continued during the CANUSA Program. These studies also used pheromone trapping to help characterize specimens. Dang (1985) developed a key to adult males of Canadian species using morphology of the aedeagus (length of apical spine and number of spicules) along with body size and color. This key may offer some improvement over previous keys, but must be tested in practice. DeBenedictis (personal communication) described a number of morphological characters in samples of 40 populations representing all the major entities found west of the continental divide in the United States. His results show promise of greatly improved understanding of the variation and relationships among the species involved. Although "all characters seem to be broadly overlapping," they may provide a method of differentiating sympatric populations (J.A. DeBenedictis, personal communication). By using cluster analysis, he obtains reliable separations in some cases. In spite of these new studies, the hope of an easily used key to identify individuals of all the North American species may not be in sight.

In summary, traditional morphological characters are not very helpful for reliable identification of individual insects in this group of closely-related *Choristoneura* species. In most characters there is a wide range of intraspecific variation in all stages. The range of interspecific differences is only slightly greater and there is considerable overlap in most comparisons. Nevertheless, experienced observers can identify the separate entities provided they have an adequate series of specimens. Chances of success are better with some species than with others. Host differences assist in differentiation, but as most of the species will develop on several hosts, the host on which individual insects are found may be of little assistance in identifications. Where sympatries exist, differentiation can be difficult, as between *orae* and *occidentalis*, or it may be readily achieved as between *I. ponderosana* and *occidentalis*.

Developmental Differences

Field and laboratory studies of members of this difficult group have provided evidence to support their taxonomic separation and yielded clues to the relationships among them and to their evolutionary development. The most important of these results and their implications for taxonomy are discussed here.

Size and Development Rates

All coniferophagous *Choristoneura* species are characterized by wide variations in size and development rates as well as in color and pattern. Larval development rates and instar number have both been shown to be polymorphic (Stehr 1964; Schmidt and Lauer 1977). Under natural conditions the range of this variation is very wide so that detection of significant differences is difficult, but controlled laboratory conditions eliminate much of the variation and have permitted some unraveling of the physiologic and genetic mechanisms involved.

Polymorphism in development rates probably shows first in patterns of second-instar emergence following diapause, and has been demonstrated in *fumiferana* (Thomas 1976). Interspecific differences in emergence times have also been demonstrated. Smith (1953) reported a differential of 5.44 days between mean emergence times of *fumiferana* and *pinus* under laboratory conditions. Differences among emergence times for *fumiferana, biennis*, and *occidentalis* were also noted but were markedly smaller (S.G. Smith, unpublished). Schmidt (1977) reported differences in thermal requirements for diapause termination and also for post-storage emergence times under laboratory conditions between *occidentalis* and *retiniana*. Volney et al. (1983b) reported both inter- and intra-populational differences in emergence times expressed under controlled conditions between natural populations from southern Oregon where *retiniana* and *occidentalis* and their natural hybrids are found. Common to all these differences is the lack of clear separation between groups caused by wide intraspecific variation.

In *fumiferana* average larval development rates of males are faster than females, both for foliage-fed insects under natural conditions and for laboratory-reared, diet-fed insects (Stehr 1954; Harvey 1974). The longer development time in females is associated with their larger size at maturity (Harvey 1974). This rate difference is reversed during the pupal stadium in both *fumiferana* and *pinus* (Sanders 1975; Smith 1953) and in several other species (S.G. Smith, unpublished) and probably for all members of the group. This rate reversal results in females eclosing nearer to the eclosion times of males (Smith 1953; Sanders 1975). Stehr (1964) concluded that larval development rates represented a polymorphism of a quantitative character. Larval development rates were skewed and multimodal in distribution and thus, not appropriately analyzed by normal statistics (Stehr 1964). Further evidence of the polymorphic nature of larval development was provided by results of Schmidt and Lauer (1977) who documented the occurrences of supernumerary instars in *retiniana*, *occidentalis*, and *fumiferana*. They presented evidence of sex and specific differences in numbers and proportions of instars among the three species. The number of instars was also influenced by dietary quality.

Interspecific differences in development rates have been demonstrated. From field observations and laboratory experiments, Smith (1953) showed differences between development rates of *fumiferana* and *pinus*. Stehr (1964) reported significant differences in laboratory development rates among *fumiferana*, *biennis*, *occidentalis*, and *orae*. All species were polymorphic but not all differences between species were significant: *occidentalis ≠ fumiferana, biennis, orae; orae ≠ fumiferana, occidentalis*; but neither *fumiferana* nor *orae*, although different from each other, was different from *biennis*.

Other differences may be recognized when the full group of conifer-feeders are analyzed on a comparable basis. Most of the development rate differences are not great and because of the wide variability in all species, it is unlikely that the differences themselves can contribute greatly to integrity of any of the species.

Second Diapause

The biologies of the coniferophagous *Choristoneura* are very similar. They are generally univoltine with a larval diapause at the beginning of the second instar before any feeding has occurred. This diapause appears to be genetically fixed in all species and to occur independently of environmental cues (Harvey 1957). Development of nondiapause strains is possible in laboratory rearings of some species. It is readily achieved in *occidentalis* (Lyon et al. 1972) but only by continued selection in *fumiferana* (Harvey 1957). Nondiapause development of *pinus* and *C. carnana californica* (then identified as *C. lambertiana californica* Powell) has also been reported (Lyon et al. 1972) but little is known of this possibility in the other species.

In early field studies of budworm in the mountainous areas of western Canada it was noticed that heavy defoliation and moth flights occurred only on even-numbered years. Such behavior is typical of the species named *biennis* and until recently, this biennial cycle appeared to be monophasic with all populations being readily noticeable only in even-numbered years. Recently, however, extensive feeding and moth flights have been reported in odd-numbered years in the East Kootenays (Van Sickle et al. 1981). These populations represent the biennial cycle in its other phase and demonstrate that populations in both phases do exist, although in different areas.

Insects with a biennial cycle have two periods of obligate diapause during their larval development, the second occurring at the end of the third instar (Shepherd 1961). Shepherd considered "cool temperatures during insect development to be responsible for the selection and maintenance of populations with a second diapause." However, the incidence of second diapause is virtually 100 percent in all laboratory rearings of *biennis* even when conditions are favorable for uninterrupted larval development. It is considered, therefore, to be genetically fixed and its inception relatively little influenced by environmental cues (Harvey 1967). This characteristic two-year cycle was used to support the taxonomic separation of *biennis* from related *Choristoneura* (Freeman 1967).

The other *Choristoneura* species in which a significant level of second diapause occurs is *orae*. Harvey (1967) reported a mean incidence of 82.3±2.6 percent second diapause under laboratory conditions in *orae* collections from near Kitimat, British Columbia (Harvey 1967). In the past few years, infestations of budworm in white spruce forests near Anchorage, Alaska have been considered to include *orae* and possibly other species (Holsten 1980). Incidence of second diapause under laboratory conditions in progenies of collections from this area (supplied by E.H. Holsten) has been generally similar (Table 5) but slightly lower than among collections from Kitimat (67.8±5.1 percent cf. 80.7±3.0 percent; $p < .05$) (the latter mean includes

Table 5.
Incidence of second diapause in laboratory-reared progenies of collections of *C. orae*

Source	Year	Code	No. Fams	Sec. Diap (%)	S.D.	Range (%)
Kitimat, B.C.[1]	1961	CEM	2	96.7	4.7	93.4 – 100.0
	1961	TIM	5	80.9	18.4	47.3 – 96.8
	1962	MIT	8	69.5	13.0	48.4 – 93.7
	1962	TAM	6	89.0	6.8	80.1 – 97.6
Kispiox, B.C.[2]	1982	KIS	2	86.7	13.9	76.9 – 96.4
Total from Kitimat area			28	80.7	15.6	47.3 – 100.0
Anchorage, AK[3]	1979	ANA	5	90.7	13.2	73.3 – 98.4
	1979	ANK	5	80.7	14.5	58.6 – 95.5
	1980	ANE	6	60.8	26.7	25.0 – 87.2
	1981	ANC	9	55.3	24.9	13.0 – 98.4
Total from Anchorage area			24	67.8	25.0	13.0 – 98.4

[1] Data from Harvey 1967.
[2] Collection made by P.T. Dang, Ottawa.
[3] Collections made by E.H. Holsten, Anchorage.

two recent values from Kispiox)(G.T Harvey, unpublished). As in the earlier studies there was considerable variation among families (range 13.0 to 100 percent second diapause). Compared to *biennis*, the incidence of second diapause in *orae* is not only lower and more variable among families, but it also appears to be more susceptible to influence by environmental conditions. Long days in the parental generation substantially reduced the incidence of second diapause in the second laboratory generation (Harvey 1967). More studies are needed to elucidate the effects of environmental factors on second diapause, particularly in *orae*.

The occurrence of second diapause among other *Choristoneura* species was first reported for *fumiferana* (Harvey 1958). The incidence of this behavior among first laboratory generation (L1) progenies of *fumiferana* collections from many locations in eastern and central Canada was reported as 3.6±1.7 percent (Harvey 1961). Percent second diapause in families ranged from 0 to 30. Harvey suggested that low levels of second diapause probably occur naturally in *fumiferana* populations. Incidence of second diapause in laboratory rearings of *fumiferana* is affected by environmental factors such as relative humidity during egg development, temperature during prediapause, length of storage, and temperature during development (McMorran 1972). Unfavorable diet and other conditions during larval development can also increase second diapause (G.T. Harvey, unpublished). Higher levels of second diapause have been noticed in collections from the far northwestern parts of the distribution of this species. The average incidence of confirmed second diapause in L1 families (55) from 15 locations between north latitude 55.0° and 64.4° and longitudes from 100° to 130° averaged 8.6±1.6 percent (G.T. Harvey, unpublished). Values in individual families ranged from 0 to 56 percent, however, there was no evidence of a cline in incidence of second diapause with increasing latitude or longitude.

Second diapause is generally less common in *occidentalis*. Harvey (1967) reported 4.1 percent second diapause in this species reared in 16-hour photoperiod and less in longer photoperiods. Collections used in that study originated from Oregon and Montana. Other stocks from southern British Columbia had similar low incidence of second diapause. Recently, there have been reports of low levels (1.2 to 2.8 percent) of "large larvae" emerging from bole samples collected in north-central Washington (L.C. Beckwith and T.H. Egan, personal communication). This appears to be evidence of the natural occurrence of second diapause in western budworm south of British Columbia. Budworm from near Ashcroft, British Columbia (collected by

P.T. Dang, 1982) showed 12 to 70 percent second diapause among L1 families on artificial diet under laboratory conditions (G.T. Harvey, unpublished). Although less second diapause than showed by *orae* or *biennis*, these levels suggest the possibility of increasing levels of second diapause in the northern parts of the distribution of *occidentalis*. It may also be evidence of increasing responsiveness to environmental effects.

In summary, second diapause, which typifies *biennis* occurs to some degree in most of the coniferophagous *Choristoneura* (Harvey 1967). It appears as an obligate developmental arrest in *biennis*, to a lesser extent in *orae*, and at a low frequency in the other members of the group. In *orae*, *fumiferana*, and *occidentalis*, there may be a facultative component that, under the influence of environmental cues received by the larvae or their parents, increases the incidence of this behavior (Harvey 1967) and is evident particularly in the northern parts of their ranges. The apparent relationship between degree of genetic fixation in these species and climate within their distributions is obvious. However, even in wild populations of *fumiferana* and *occidentalis* where the environment is more favorable, some remnant of second diapause is retained.

As a means of separating closely related taxa, incidence of second diapause is not useful because it is not clearly diagnostic of any species. Nor does development without this second diapause clearly differentiate any species. Increased levels of second diapause in *occidentalis* and *orae* in parts of their distribution further complicate differentiation of these species from *biennis* in central British Columbia where their distributions adjoin or overlap.

Biochemical Systematics

The relatively new field of biochemical systematics has provided additional methods of detecting and evaluating relationships among taxa. The discovery of communication systems involving pheromones has afforded one such opportunity. Enzyme variants known as isozymes give a further dimension to studies of closely related entities.

Pheromones

Sex pheromones are helpful in interpreting taxonomic problems of many groups because of their specificity (Roelofs and Comeau 1969; Roelofs and Brown 1982). The usefulness of pheromones in detecting and monitoring population levels and in pest management has increased the interest in their study in many insects, including the conifer-feeding *Choristoneura*. Because it has implications for budworm taxonomy, an overview of our current knowledge of the sex pheromones of the various budworm species will be included here. Sanders (1971a) reported results of field and laboratory tests of several budworm species and was among the first to comment on their implications for the taxonomy of the various entities. He noted the absence of pheromone differences among *fumiferana*, *occidentalis* and *biennis*, and pointed to the need for detailed studies in the areas of potential contact of these entities. In an intensive series of field tests, Sanders et al. (1977) further elucidated pheromone relationships among seven *Choristoneura* species. They also demonstrated the differential attractiveness of many hybrids and back crosses among members of the group, and showed the presence of interference of attraction between certain species within the group.

Since the first studies of pheromones considerable progress has been made towards understanding their biochemistry in most of the coniferophagous *Choristoneura*. Techniques used to identify pheromones include chemical analysis of pheromone glands or effluvia and trapping tests using virgin females or extracted or synthetic chemicals. The pheromones of these *Choristoneura* are now known to consist principally of mixtures of mono-unsaturated C-14 compounds. The primary component of the eastern spruce budworm is Delta-11-tetradecenal with isomers in the ratio 95-96 percent (E): 4-5 percent (Z) (Sanders and Weatherston 1976; Silk et al. 1980). Other species contain these compounds or the related tetradecenyl-acetates or -alcohols.

Compounds identified in effluvia of several species are shown in Table 6. Components identified in *fumiferana* and *occidentalis* are the same, but the proportion of the (Z)- isomer differs by a factor of nearly double. Effluvial components of *biennis* and *carnana* have not been determined, but appear to be similar to *fumiferana* and *occidentalis*. Other species, including *retiniana* and the pine-feeding species, form a second group having -acetate as the major component. Thus although *retiniana* and *orae* share many characteristics with members of the spruce-fir feeding group, in pheromone constitution they align more closely with the pine-feeding species. The principal pheromone of the European *C. murinana*, although similar to the pine-feeding group, has the (Z)- isomer in preponderance (Priesner et al. 1980; Burghardt et al. 1980).

Field trapping tests permit measurement of responses of wild males in their natural habitat to blends of purified components identified in effluvia. Results of such experiments by several groups (Table 7) largely confirm Table 6. The similarity of pheromone composition in *biennis*, *fumiferana*, *occidentalis*, and *carnana* is clearly shown, as well as their differentiation from *pinus*, *orae*, and *retiniana* which are indistinguishable among themselves. Trapping tests also permit assessment of negative effects — inhibition or interference with

Table 6
Compounds identified in pheromone *effluvia* from glands of female *Choristoneura* (includes gland washes and entrainment)

	-11-14:ACET (%E)	-11-14:AL (%E)	-11-14:OH (%E)	Saturated AC	Saturated AL	Saturated OH	References
bie							
ora	91(90)	+	9(90)				5.
fum	+	100(96)					1.
		100(95)			+		6.
occ	+	100(92)					2.
	16(89)	53(92)	31(88)				7.
car							
ret	90(92)		10				3.
pin	90(85)		10(85)				8.
sub (OR)	90(60)	0	10(60)				4.
pon (CO)	85(70)	0	15(70)				
'lam' (MA)	80(75)	+	20				

1. Sanders and Weatherston 1976.
2. Cory et al. 1982.
3. Daterman et al. 1984.
4. Daterman et al. in Ms.
5. Gray et al. 1984.
6. Silk et al. 1980.
7. Silk et al. 1982.
8. Silk et al. 1985.
9. Sanders et al. 1974.

Table 7
Blends of major pheromone constituents attractive to male *Choristoneura* spp. in field trapping tests

	-11-14:ACET (%E)	-11-14:AL (%E)	-11-14:OH (%E)	References[b]
bie		[100(95)][a]		9.
ora	91(90)		9(90)	5.
fum		100(95-97)		1.
occ		100(92)		2,11[a].
car		=occ		10.
		100(92)		12.
ret	90(92)		10	10.
pin	90(85)		10(85)	8.
sub	90(60)		10(60)	4.

[a]. No range of E:Z blends tested.
[b]. References listed in Table 6. Additional references below.
10. Powell and DeBenedictis 1982.
11. Liebhold and Volney 1984a.
12. Liebhold and Volney. 1985.

attractiveness produced by small amounts of additional compounds. Pheromone specificity in some groups may depend on the identity of minor components rather than on the major compounds. Optimum pheromone blends (Table 7) released at comparable rates are still somewhat less effective than virgin females in trapping tests of all species, with the possible exceptions of *retiniana* (Daterman et al. 1984) and *subretiniana* (Daterman et al. in press).

Using virgin females to trap males in their normal habitat provides the most useful tests for exploring taxonomic relationships. Because of phenological differences among native habitats, laboratory-reared females must be used for many of such tests. Results have been assembled in Table 8, in which trap catches have been expressed as a percentage of catches by conspecific females in the same experiment. Unpublished results of Powell and DeBenedictis (1982) have been included in the table as they represent some new combinations; however, because of the nature of their tests, results are shown only as + or –.

These results are consistent with those of the two previous tables and show the clear separation of the species into two groups, differentiated by the identity of the principal component of their pheromones: aldehyde *vs* acetate. Affinities are closer within the groups than between. Even where the major pheromone components are distinctly different, some low response by males of other species is frequently recorded, but generally there is little cross-attraction. However, in no case does the catch of other males by virgin females equal the catch of their own species. The closest affinities are found in the aldehyde group: *fumiferana, occidentalis, biennis, carnana*. Nevertheless, there is evidence for some differences within this group. In particular, the catches of *occidentalis* and *biennis* males by *fumiferana* females appear to be significantly less than those of *fumiferana* males. These differences could arise in part from differences in preferred isomer ratios (Table 7), or from the presence of other minor components (Alford et al. 1983; Alford and Silk 1984).

Table 8
Catches of feral male *Choristoneura* spp. by virgin females of their own and other species, expressed as percentage catch of conspecific female

		Male						
		fum	*occ*	*car*	*ret*	*pin*	*sub*	*pon*
Female	*bie*	60 [2] 64 [1]						
	ora	0 [1,2]				18 [1] 19 [2]		
	fum	100	91 [2]		21 [2]	1[1]–2[2]	0 [2]	
	occ	53 [1] 55 [2]	100	+ + [3]	9 [2] – [3] 0 [4]	0 [2]	2 [2] – [3]	– [3]
	car		+ + [3]	+ + [3]	– [3]			
	ret	0 [1,2]	5 [2] – [3]	– [3]	100	1 [2] 4 [1]	4 [2]	– [3]
	pin	0 [1,2]	32 [2]		25 [2]	100	3 [2]	
	sub	0 [2]	38 [2] – [3]	– [3]	0 [2] – [3]	0 [2]	100	– [3]
	pon							+ [3]

[1] Sanders 1971a.
[2] Sanders et al. 1977.
[3] Powell and DeBenedictis 1982 — catches shown as + +, + or –.
[4] Liebhold et al. 1984b.

Affinities among the acetate-alcohol group are considerably more distinct — perhaps more so than might be expected from what is known of the compounds involved (Table 7). In the case of *subretiniana vs retiniana*, where there is virtually no cross-attraction, the difference in blend of E:Z appears to be the significant factor.

In summary, although pheromones are generally similar among all the conifer-feeding *Choristoneura*, there are important differences and in every case where tests have been made, virigin females are more attractive to males of their own species than to those of any other. Sanders (1984) presented evidence implicating the presence of as yet unidentified components in the pheromone of *fumiferana*. It is probable that minor components are present in the pheromones of the other species. Identification of these should enable further discrimination among the species. Further studies are also needed to determine the function of pheromone components on male behavior and to determine their contribution to species integrity. In several cases the lack of cross-attractiveness appears sufficient to limit matings in areas of sympatry. In other cases it does not, for example, between *retiniana* and *occidentalis*, as hybrids between these two species have been demonstrated under field conditions (Liebhold et al. 1984). Unfortunately, some important field tests, such as the cross-attractiveness of *occidentalis* and *biennis*, have not been completed. The additional tests would be a valuable contribution to understanding the relationships among these very closely related species.

Further use of pheromone baited traps may be expected to contribute to our knowledge of the distributions of all species. Moths, however, may disperse appreciable distances from their feeding sites (Greenbank et al. 1980; Dobesburger et al. 1983). Thus, although trapping results may be helpful in mapping, they must be used along with other observations on moth movement, etc. Use of this technique is just beginning, but it promises valuable results, particularly in British Columbia, to help map limits of *orae* relative to *fumiferana, biennis*, and *occidentalis*.

Isozymes

Gel electrophoresis of enzymes is widely used in many Genera and has proved useful in species discrimination and identification and in developing hierarchical classifications (Berlocher 1984). In the past several years this technique has been used to measure interpopulational variation and interspecific differences among coniferophagous *Choristoneura*. Isozymes in Lepidoptera are usually measured in larvae, as in the studies reported below, but can also be studied in other stages, such as adults (Harvey 1980).

The first use of gel electrophoresis in *Choristoneura* was by May et al. (1977). They measured variation among *fumiferana* populations spanning a 250 km (150 mi.) distance in Maine, but could find no differences among those sites. Wilhite and Stock (1983) measured genetic variation for 16 loci at 14 sites among outbreaks of western spruce budworm in Idaho and Montana (maximum separation about 450 km [280 mi.]). By cluster analysis of genetic distances and study of shared rare alleles, they were able to identify three groups of sites. Insects at sites within the groups were genetically more similar to each other than between groups. These differences were used to help interpret the history of outbreaks in the area. However, although the intergroup differences were significant, genetic distances among all sites were low, averaging only 0.038. A single collection from New Mexico was markedly different, having a mean genetic distance from the other 14 locations of 0.305. Variation in *fumiferana* may be even lower than in *occidentalis*. Mean genetic distance found among 18 locations spanning 4000 km (2,500 mi.) east to west across Canada was 0.0038 (based on 10 polymorphic loci) (Harvey 1982).

Gel electrophoresis has also been used to explore differences among *Choristoneura* species. All species examined have similar isozymes (Stock and Castrovillo 1981), as shown by the identity of the principal alleles of 20 enzymes (Table 9). In six species, differences among 15 loci were negligible; at 5 additional loci all but one species had the same principal allele (Castrovillo 1982). There were, however, important differences between species in frequencies of alleles at some loci (Stock and Castrovillo 1981). For example, the most common allele of AAT-1 in *fumiferana* (designated 1.00) is rarely found (> 1%) in any of the other species (Table 10).

Table 9
Identity of principal alleles of enzymes in *Choristoneura* species[1]

LOCUS	*bie*	*ora*	*fum*	*occ*	*ret*	*pin*
AAT-1	4	4	2	4	4	4
EST-1	2	2	2	2	2	2,3
EST-2	3	3	3	3	4	3
EST-5	6	6	3	6	6	6
LAP-2	1	1	1	1	1	1,2
11 LOCI:	ADH, CK, EST-3, EST-6, IDH-1, LAP-3, LDH, MDH-1, MDH-2, ME, PGI: same principal allele in all species.					
4 LOCI:	AAT-2, AGPDH, 6PGDH, XDH: monomorphic in all species.					

[1] Alleles identified by number. Data of Castrovillo, 1982. Divergent principal alleles underlined.

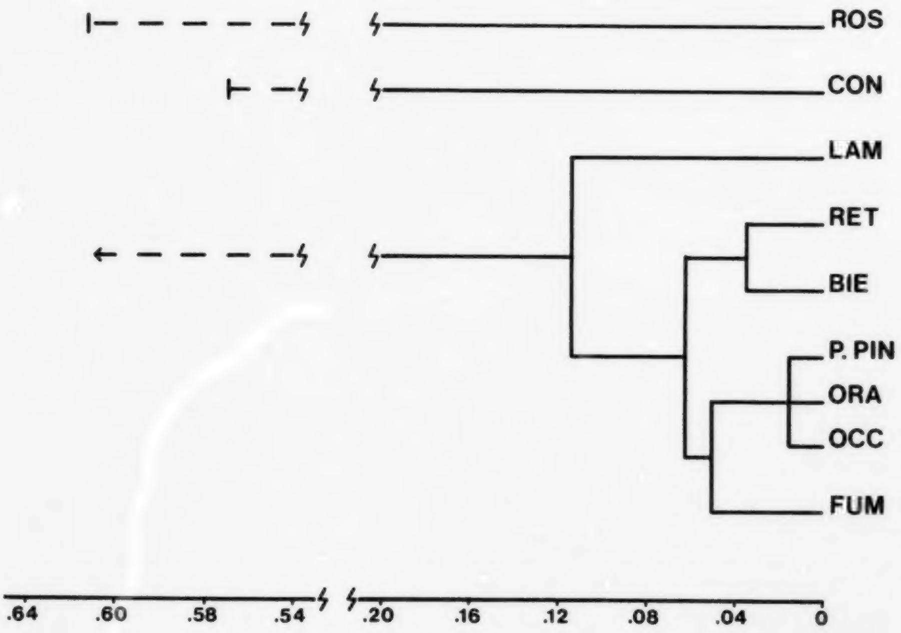
Table 10

Frequencies of alleles of AAT-1 among *Choristoneura* spp

ALLELE	*bie*	*ora*	*fum*	*occ*	*ret*	*pin*	*'lam'*
0.41	.02	0	0	0	0	.01	.03
0.62	.94	1.00	.05	.97	1.00	.99	.95
0.81	.04	0	.30	.02	0	0	.02
1.00	0	0	.64	.01	0	.01	0
1.18	0	0	.01	0	0	0	0

Data from Stock and Castrovillo. 1981. Castrovillo. 1982. and Harvey 1982 Most common allele underlined

Genetic distances among species can be a measure of taxonomic separation. Stock and Castrovillo (1981) used allele frequencies at 18 loci to calculate genetic distances among samples of *occidentalis, retiniana, fumiferana, biennis* and *l. ponderosana*. Values ranged from 0.007 to 0.173 (mean 0.076). More recently Castrovillo (1982) reported enzyme frequencies and genetic distances for seven members of the *Choristoneura* group and expressed their interrelationships in the form of a phenogram (Figure 4). Genetic



Phenogram based on NEI'S GENETIC DISTANCE VALUES

Figure 4. Phenogram showing interrelationships of *Choristoneura* spp. based on Nei's Genetic Distance values. Full names in Table 1. ROS = *C. rosaceana* (Harris): CON = *C. conflictana* (Walker). Data for coniferophagous species from Castrovillo (1982). Data for ROS and CON from Harvey (1982).

distances for the broad-leaved-feeding *C. rosaceana* and *C. conflictana* compared to the conifer-feeding species, based on studies by Harvey (1983a), have been added to Figure 4. For comparison, mean genetic distances among subspecies or semispecies of the *Drosophila willistoni* Group are about 0.230 and about 0.581 among sibling species (Ayala 1975). These values should only be considered as rough guides as the "cut-off point" between subspecies and sibling species varies among taxonomic groups (Castrovillo 1982).

From Figure 4, it is apparent that genetic distances among *C. rosaceana* and *C. conflictana* and the conifer-feeding group are of the same order as differences among sibling species found by Ayala (1975). Also genetic distances among members of the conifer-feeding group are markedly less than those usually encountered among sibling species. Stock and Castrovillo (1981) interpreted this to mean that "reproductive isolation among at least some members of the group is not well established and that definition of some of the entities as species is artificial." Interspecific distances are larger, however, than intraspecific distances among separate populations of species where they have been measured (*occidentalis*: Wilhite and Stock 1983; Castrovillo 1982; *fumiferana*: Harvey 1983a). Taking this into account as well as the conservative nature of electrophoresis data, Castrovillo (1982) concluded that the data support the assignment of species status to *fumiferana, pinus, biennis, occidentalis, I. ponderosana*, and *retiniana*. Unfortunately, no *carnana* samples were included in his study. But he also found that *orae*, as represented by a collection from Anchorage, Alaska, could not be differentiated from *occidentalis* on the basis of their isozymes. He considered *fumiferana* to be the most genetically differentiated of all the *Choristoneura* feeding on conifers (Castrovillo 1982). He noted the pronounced dissimilarity in one enzyme (AAT-1) between *fumiferana* and all other species (Table 9). Preliminary analyses of AAT-1 frequencies in *fumiferana* compared to *orae*, and *occidentalis* populations indicate very little, if any, gene flow (Harvey 1982). This clear difference should be exploited to determine the boundaries of this species where they approach other species, such as *occidentalis, orae* and *biennis* in the north and west of its range.

It must be recognized that the ability of electrophoresis to differentiate taxonomic entities is limited and depends on the number and nature of the loci measured. Furthermore, standard electrophoresis does not detect all protein differences that are present (Berlocher 1984), although newer techniques have partly overcome this problem. Thus, although real differences may not be detected, those differences that are found are real, and species based on them are valid (Berlocher 1984). Failure of electrophoresis results to support existing taxonomic separations does not invalidate the separations. To date only standard electrophoresis techniques have been used on the *Choristoneura* group; studies using the newer techniques should improve our understanding of their relationships.

Other Biochemical Differences

Other evidence of differences among *Choristoneura* species has been obtained. Robertson et al. (1978) tested several insecticides against six species and found significant differences among them. As a result they warned against extrapolating the insecticide response of one species to another species. Cunningham et al. (1983) found evidence of differences between *fumiferana* and *occidentalis* in susceptibility to two baculoviruses. Stock and Robertson (1980) found that in laboratory stocks of *occidentalis, retiniana*, and *fumiferana*, within species responses to acephate could be as large as differences among species. Differences of this type may be correlated with demonstrable isozyme differences (Stock and Robertson 1980) although this will not always be so. The significance of such differences in relation to species differentiation is not easy to ascertain, but with further study they may provide evidence to aid in the interpretation of taxonomic problems.

Reproductive Isolation

Taxonomic problems among these *Choristoneura* species arise in part from the difficulty in assigning individual insects to species, and also from the paucity of knowledge of reproductive isolation among them. Smith (1953) evaluated the known components of reproductive isolation operating between *fumiferana* and *pinus*. Although the subsequent awareness of pheromones and their function has led to better understanding of some of the isolation mechanisms, the principal components have not changed. Liebhold et al. (1984) distinguished those factors that act before mating from those that act after mating and concluded that the latter are of minor importance for reproductive isolation in this group of species. Pre-mating factors include ecological, temporal and behavioral components. Of these the latter appears to constitute the main barrier between sympatric species of *Choristoneura* which have been studied (Smith 1953; Sanders 1971b; Liebhold et al. 1984).

Post-Mating Factors

Laboratory studies of genetic relationships and characteristics of hybrids provide information on post-mating factors itemized by Smith (1953). These include mechanical and gametic isolation and inviability, sterility and breakdown of hybrids.

There are 30 haploid chromosomes in *fumiferana*, *biennis* and *occidentalis* (Smith 1944, 1945; Ennis 1976). Smith (1944) showed that the female is the heterogametic sex and Ennis (1976) confirmed that the sex system is XY♀:XX♂. More recent studies (T.J. Ennis and G.T. Harvey, unpublished) confirm the same chromosome number for most of the other members of the group. Similar studies of many of the F1 hybrids (T.J. Ennis and G.T. Harvey, unpublished) failed to detect any structural differences in the chromosomes examined.

Both inter- and intra-specific matings within the budworm group are readily achieved in the laboratory when a pair of moths is placed in a small container along with suitable foliage (Stehr 1954; Volney et al. 1983a). Smith (1953) reported that under these conditions, *pinus* and *fumiferana* were readily crossed and produced fertile hybrids. Campbell (1967), Harvey (1967), and Harvey and Roden (1979) documented successful laboratory matings in several combinations among *fumiferana, biennis, occidentalis, orae, pinus*, and *retiniana* (= *viridis*), but presented little evidence on comparative mating success. Sanders et al. (1977) reported mating success of crosses and backcrosses among some of the species. More recently, Volney et al. (1984) reported successful hybridization between *occidentalis* and *retiniana* in the laboratory and in the field. These results and others (G.T. Harvey, in preparation) show that fertile matings have been obtained in almost all combinations, and that crosses of F1 adults leading to the F2 generation are also successful. Conspecific matings had a somewhat greater success rate than interspecific crosses, and among the former, mating success was higher in the spruce-fir feeding than in the pine-feeding species, but these differences were not great (G.T. Harvey, in preparation). Sanders et al. (1977) reported good mating success and viable progenies in all of the 16 backcrosses they attempted. Liebhold et al. (1984) found that hybrids and backcrosses between *retiniana* and *occidentalis* were readily obtained and generally fertile. Although some aspects of these relationships have not been tested rigorously, the existing evidence indicates no mechanical or gametic isolation among members of the group.

Fertile hybrids have resulted from all combinations and have shown good viability and survival under laboratory conditions. Thus there is little, if any, evidence of any hybrid inviability or sterility. Nevertheless, there is evidence among the hybrids of genetic interactions in egg weights, development rates, incidence of second diapause and pheromone chemistry, and these may reduce overall viability.

Female progeny from *occidentalis* × *fumiferana* crosses laid fewer and much larger eggs than those from *fumiferana* × *occidentalis* crosses (Campbell 1958) (Table 11); mean Ei values for *occidentalis* are close to those of *fumiferana* (0.165: Harvey 1983c) and intermediate between those of the reciprocal hybrids. Neither mean pupal weights of F1 females nor mean weights of total egg mass differed between these reciprocal crosses. Similar effects were noted in reciprocal crosses between *fumiferana* and *pinus* (Table 11) and *occidentalis* and *pinus* (Campbell 1958). These results have been confirmed and similar effects noted in crosses between other species, particularly those involving *fumiferana* (G.T. Harvey, in preparation).

Table 11
Size and fecundities of selected F^1 hybrids[1]

Cross	n[2]	Pupal wt[3] mg	E_i[4] mg	Fecundity	Egg Mass[5] mg
occ × *fum*	18	105	0.277	126	34.9
fum × *occ*	12	117	0.133	256	34.0
pin × *fum*	16	79	0.228	86	19.6
fum × *pin*	13	83	0.105	160	16.8

[1] Data of Campbell 1958 (Campbell's designations interpreted 'D' = *occidentalis*; 'B' = *fumiferana*; 'J' = *pinus*.)

[2] n = number of families

[3] Mean, F^1 female pupae only; minimum 16 pupae per family

[4] E_i values (Harvey 1977) calculated from Campbell, 1958

[5] Fecundity × E_i

Such wide differences in egg weight will probably have consequences for survival under natural conditions. Harvey (1983b) showed that larvae from heavier eggs are better able to survive harsh or prolonged winter conditions than larvae from lighter eggs. This suggests that if hybridization between *fumiferana* and *occidentalis* does occur in the field, the progeny of a *fumiferana* female would be more likely to survive than the progeny of the reciprocal cross. The resultant low numbers of survivors would restrict gene flow between these two species and may also occur with other sympatric species.

Differences in development rates occur in *fumiferana* × *pinus* crosses (Smith 1953) (Table 12). Development is slower in both larval and pupal stadia of both sexes of *pinus* than of *fumiferana*, and the sex differential in total time to eclosion is small, 4.5 (*pinus*) cf 2.0 days (*fumiferana*). Development times in the hybrids were intermediate between the two parental values, but because developmental rates are sex-linked (Smith 1953), the sex differential is markedly different in the two reciprocal crosses (Table 12). In the cross *fumiferana* × *pinus*, the difference in development rate and sex-linkage combine so that males eclosed 8.6 days before females. Although this differential may be less under some field conditions, it probably would greatly limit the frequency of crosses or backcrosses by such

Table 12
Mean development times of two species and their F¹ hybrids[1]

	Females	Males	Difference
fum	46.4	44.4	2.0
fum × *pin*	55.1	46.5	8.6
pin × *fum*	49.3	49.1	0.2
pin	65.0	60.5	4.5

[1] Development times = days from emergence to adult (mean). (Data from Smith 1953.)

F1 adults. In the other hybrid (*pinus* × *fumiferana*) the two effects counteract each other and the differential in time to eclosion was only 0.2 days. Crosses and backcrosses among such F1 adults should therefore be possible under natural conditions. Differential effects in development rates occur in other hybrids among *biennis, occidentalis, fumiferana*, and *pinus* (S.G. Smith, unpublished), and similar disturbances of development times have been reported for hybrids among other Lepidoptera (Oliver 1983).

Second diapause is uncommon in most *Choristoneura* and is therefore not expected in most hybrids. However, where one of the parents is a species with a high incidence of second diapause (e.g. *orae* or *biennis*), the progency show intermediate levels (Harvey 1967). Thus in areas of sympatry (Table 4) intermediate levels of second diapause are expected in the hybrids formed. Secondary effects in such hybrids, such as the sex differential in incidence of second diapause in *orae* × *fumiferana* hybrids (more females than males enter second diapause, Harvey 1967), may affect success of the hybrids and reduce the extent of hybridization. Nevertheless, the higher incidence of second diapause in *occidentalis* and *fumiferana* in areas adjoining or close to the distributions of *orae* and *biennis* could be evidence of some gene flow into these normally non-diapausing species.

Pheromones released by hybrid individuals must be considered post-mating factors, as they may influence the likelihood of successful F1 matings. However, little is known of the chemical identity of pheromones of hybrids or of their attractiveness to other species or hybrids. Sanders et al. (1977) found that hybrids and backcrosses between *fumiferana*, an aldehyde-releasing species, and *pinus*, an acetate-releasing species, produced females attractive to one or other of the parent species or to none, but never to both. Males of both types of *fumiferana* × *pinus* hybrids, however, responded to females of both parental species. These results suggest sex-controlled inheritance and expression, but Liebhold et al. (1984) found backcrosses of hybrids between *retiniana* (acetate pheromone) and *occidentalis* (aldehyde pheromone) were intermediate between the pure lines in their pheromone specificity. This contrasting result may be further evidence of differences in pheromone physiology between similar species. The part played by pheromones of hybrid insects in enhancing or reducing the extent of reproductive isolation of sympatric budworm species is not known but warrants further study.

Although the study of isozymes has not included any hybrids, none of the loci found among the coniferophagous species has been fixed for unshared alleles (Castrovillo 1982). Such loci would cause unique band positions in hybrids and unpredictable enzyme function that, ultimately, could act as a barrier to gene flow. All loci studied in these species have some shared alleles so that results expected among hybrids are predictable and unlikely to have appreciable effects on survival or development.

Pre-Mating Factors

Geographic or spatial factors contribute to the pre-mating isolation of some *Choristoneura* species. For example, although *orae* and *retiniana* are very closely related and share the same pheromone, their distributions are widely separated. The distributions of *biennis* and *occidentalis* are contiguous or overlapping in east-central British Columbia but they appear to be spatially separated by altitudinal differences; related temporal differences and the two-year cycle of *biennis* undoubtedly reduce the likelihood of hybridization between these two species, even though their pheromones appear to be very similar.

For those species that are sympatric (Table 4), reproductive isolation must be achieved by other mechanisms. Differences in host preference may reduce opportunities for hybridization. As adult females of most of the species appear to remain on their host tree for mating, differences in phenology and location of preferred hosts may reduce the extent of hybridization between some sympatric pairs, particularly where different host groups are involved. Smith (1953) considered ecological isolation through host affinity contributed to the separation of *pinus* and *fumiferana*. However, foliage factors themselves were found unimportant in restricting mating between *occidentalis* and *retiniana* (Liebhold and Volney 1984b). Since none of the species is highly host specific, and the host trees of the different species are often intermixed, ecological isolation is probably of only minor importance in limiting opportunites for hybridization between sympatric budworm species.

Seasonal and temporal differences have also been implicated as contributing to pre-mating reproductive isolation among budworms. Smith (1953) documented differences in spring emergence times and in development times that resulted in significantly different eclosion times for *fumiferana* and *pinus* under field conditions. These results were confirmed by Sanders (1971b). Temporal differences in time of calling (Sanders 1971b) and mating (Smith 1953) between these two species also act to reduce chances of hybridization under natural conditions. However, there is frequently some overlap in flight times (Smith 1954; Sanders 1971b and personal communication) so that while seasonal and temporal differences appear to reduce the possibility of hybridization, they are insufficient to prevent it.

Seasonal and temporal differences do not seem any more important in the reproductive isolation of *occidentalis* from *retiniana* where they are sympatric in south-central Oregon (Liebhold and Volney 1984a). Seasonal differences in the time of first moth flights and differences in calling times were demonstrated, but overlap between species was considerable. Actual mating times in wild populations were not recorded but synchrony between the two species appears to be appreciable. In contrast to the case of *pinus* and *fumiferana*, however, positive evidence of hybridization between *retiniana* and *occidentalis* proves that temporal differences are insufficient to effect reproductive isolation between these species.

Detailed field and laboratory studies such as those reported above, have not been undertaken for other pairs of sympatric species. Such studies would furnish a useful contribution to our understanding of their interspecific relationships and could lead to refinements in their taxonomy.

Even though two species may be present and sexually active in the same space and time, hybridization may not occur. Such relationships can be explored by mate-choice experiments. Smith (1953) reported results of mate-choice tests with *fumiferana* and *pinus* and showed that even in small cages, frequencies of conspecific matings were significantly greater than crosses. He concluded that there was "an innate repugnance to cross-mating expressed solely by the females" of these two species. Based on similar studies, Campbell (1967) demonstrated differences in mating behavior among *fumiferana*, *biennis*, and *occidentalis*. Although he did not identify any barriers to hybridization, the sexual aggressiveness demonstrated by *fumiferana* appeared to preclude or greatly reduce gene flow from the other two species. Gene flow in the opposite direction appeared more likely.

The above mate-choice studies were carried out before the importance of sex pheromones to mating behavior was recognized. The failure of *pinus* and *fumiferana* to hybridize under natural conditions is now readily understood in view of the difference in their pheromones (Sanders 1971b). The demonstrated hybridization between *retiniana* and *occidentalis* despite the difference in their pheromones (Volney et al. 1984) is confirming evidence of the small part played by other pre- and post-mating factors. However, the demonstrated low level of hybridization confirms the importance of pheromones as the major component of reproductive isolation between these two species.

Evidence for the presence or absence of hybridization between other sympatric pairs of budworm species under natural conditions has not been obtained. Tests with pheromones (Table 8) lead us to expect negligible hybridization between *orae* and *biennis* or between *occidentalis* and *I.subretiniana* even where their distributions overlap. For other pairs of species, such as *occidentalis* and *biennis*, or *retiniana* and *I.subretiniana*, whose pheromones appear to be the same or very similar, other pre-mating factors must be more significant if species integrity is to be maintained. In such cases conclusions as to the relative importance of different isolating mechanisms are not warranted. In the absence of direct evidence of hybridization in these and other cases where two species are sympatric and where they appear to be separate entities, there is some justification in continuing to treat them as separate species, even though isolating mechanisms have not been identified.

Summary

The conifer-feeding *Choristoneura* constitute a remarkably successful group of insects. Although feeding exclusively on conifers they occupy many ecotones spanning a wide range of latitudes across the entire width of the North American continent. Distributions of the different species are generally well established from records dating as far back as the early 1900s. Although taxonomic problems reduce the usefulness of the very early records, more recent information is dependable and extensive. The rapidly accruing results of pheromone trapping have helped substantially to clarify species distributions. Nevertheless, distribution limits in some areas are not clearly known and the extent of sympatries for some species is poorly documented.

These species are all characterized by a high degree of variability in many attributes, some of which represent genetically controlled polymorphisms while others are environmentally produced polyphenisms. Although there are important differences among members of the group, morphological characters by which the individual species can be identified are lacking. There is a need for keys that will facilitate reliable separations of all the entities. This lack of morphological characters that separate members of the group is consistent with the closeness of the relationships among them. The close similarities are also shown by the pheromones and isozymes. The pheromones are closely-related chemically and blend differences are not great. Isozyme differences are small, with essentially no member(s) of the group having fixed or unique alleles. The closest examples of unique alleles among the enzymes tested are the two most common alleles of AAT-1 in *fumiferana*, which are rare or lacking in all other species. However, there are contradictions in affinities indicated by different criteria, and not all characters are of equal importance for reproductive isolation. For example although the isozymes of *orae* and *occidentalis* are almost identical, their pheromones are different.

Further evidence of their genetic closeness is shown by the fact that all members of the group can interbreed freely in captivity and produce viable F1 and F2 offspring. This has led to questions concerning their designation as separate species. However, many confirmed animal species are known to freely interbreed in captivity, but do not do so under natural conditions (Brown 1959; Diehl and Bush 1984). And there are potentially deleterious developmental irregularities in at least some hybrids. These irregularities are generally small and appear insufficient in most crosses to prevent gene flow in areas of hybridization, should other barriers to cross-mating be overcome. However, interspecific differences among Lepidoptera may be very small (Oliver 1979) and their expression in hybrids may be difficult to evaluate unless subjected to environmental stresses during development. Thus, the lack of readily detectable effects in these *Choristoneura* hybrids under laboratory conditions is not necessarily evidence that hybrid breakdown does not occur in the field.

Field studies, including epidemiology, indicate that members of the group are distinct non-interbreeding species. The only documented case of interbreeding in the field is the recent discovery of a low level of natural hybridization between *occidentalis* and *retiniana* in south-central Oregon. However, similar low levels of hybridization appear possible through the rest of the area of sympatry of these two species. Extensive field studies of *fumiferana* and *pinus* have failed to detect any natural hybrids, even though the area of sympatry includes the entire distribution of the latter. Natural hybridization among the other entities has not been looked for extensively, nor have the mechanisms of reproductive isolation been adequately explored for all sympatric pairs. Pheromone differences may be the most important barrier to hybridization between some members of the group in areas of sympatry, while temporal and ecological factors limit hybridization in other areas. Little is known of other mechanisms that may operate or of the interaction between different isolating mechanisms. Without better knowledge of these mechanisms, the validity of some of the separations is difficult to prove or disprove.

Affinities between species within the group are not all the same, nor do they appear to be of equal significance. The separation by host plant into spruce-fir feeders and pine feeders appears to be basic, and is accompanied by other general differences in size, extent of polymorphisms, etc. Members of the spruce-fir feeding group show quite close affinities although *fumiferana* appears to be the least closely related of the group. The lack of distinct differences suggests that specialization has not advanced very far and prompts the conclusion that the present entities separated fairly recently on the evolutionary scale. Perhaps their high variability is consistent with this low degree of specialization.

The present taxonomic status as summarized by Powell (1983) retains ten species and five subspecies. However, Powell (1980) does not consider all of these to be "reproductively isolated entities of comparable rank or integrity." Nor does there seem to be justification for some of the separations at a full specific level. Nevertheless, in spite of the difficulties in their taxonomy, most of the presently named entities are generally accepted by forest entomologists as entities. They can be separated by their hosts, by their distribution, and by their biological characteristics. The reader should not conclude that a consensus has been reached or that all the taxonomic problems among the coniferophagous *Choristoneura* have been solved and the present nomenclature is fully satisfactory. Until more extensive studies of distribution and reproductive isolation have been completed, it seems prudent to delay changes in the present status of these species. This position supports the recommendation of Powell and DeBenedictis (1982) that we "retain the named entities as now conceived until we have a much fuller understanding of the relationships among them."

The two most widespread and economically important members of the group are *C. fumiferana* and *C. occidentalis*. These two form the central focus of this CANUSA Research Symposium and the subjects of all the papers that follow. They are well separated geographically; they are probably not sympatric anywhere and they are widely recognized as good species.

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Literature Cited

Alford, A.R.; Silk, P.J. 1984. Behavioural effects of secondary components of sex pheromone of western spruce budworm (*Choristoneura occidentalis*) Free. J. Chem. Ecol. 10:265-270.

Alford, A.R.; Silk, P.J.; McClure, M.; Gibson, C.; Fitzpatrick, J. 1983. Behavioural effects of secondary components of the sex pheromone of the eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera:Tortricidae). Can. Entomol. 115:1053-1058.

Ayala, F.J. 1975. Genetic differentiation during the species process. Evolutionary Biol. 8:1-78.

Barnes, W.; Busck, A. 1920. Notes and new species. Contra. Nat. Hist. Lepid. N.Am. 4:209-278.

Baskerville, G.L. 1975. Spruce budworm: Super silviculturist. For. Chron. 51:138-140.

Batzer, H.O.; Millers, I. 1970. Jack-pine budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Forest Pest Leaflet 7. 4 p.

Benoit, P.; Martineau, R. 1973. Principaux insectes forestiers au Québec en 1972. Ann. Soc. Entomol. Quebec. 18:10-14.

Bean, J.L.; Waters, W.E. 1961. Spruce budworm in eastern United States. U.S. Dep. Agric., For. Serv., Washington, D.C. Forest Pest Leaflet 58.

Berlocher, S.H. 1984. Insect molecular systematics. Ann. Rev. Entomol. 29:403-433.

Blais, J.R. 1965. Spruce budworm outbreaks in the past three centuries in the Laurentide Park, Quebec. For. Sci. 11:130-138.

Blais, J.R. 1983a. Trends in frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13:539-547.

Blais, J.R. 1983b. Les forêts de la Côte Nord au Québec sont-elles sujettes aux déprédations par la tordeuse? For. Chron. 59:17-20.

Brandt, N.R.; McDowall, L.L. 1968. Jack pine budworm in Manitoba and Saskatchewan. 1938-1967. Canada, Dept. Forestry and Rural Development, Ottawa. Inf. Rep. MS-X-8. 24 p.

Brower, A.E. 1983. A list of the lepidoptera of Maine. Part 2. The microlepidoptera: Section 1. Maine Dept. Conservation and Dept. of Entomology, Orono. Technical Bull. 109. August 60 p.

Brown, A.W.A.; MacKay, M.R. 1943. The jack pine budworm, and the spruce budworm, *Cacoecia fumiferana* Clem. (Tortricidae). Can. Entomol. 75:207-211.

Brown, C.E. 1970. A cartographic representation of spruce budworm *Choristoneura fumiferana* (Clem.), infestation in eastern Canada, 1906-1966. Can. Dep. Fish. For., Ottawa, Ont. Can. For. Serv. Publ. 1263.

Brown, W.J. 1959. Taxonomic problems with closely related species. Ann. Rev. Entomol. 4:77-98.

Burghardt, G.; Knauf, W.; Bestmann, H.J.; Vostrowsky, O.; Koschatzky, K.H. 1980. Synthetische Sexual-Pheromone und deren inhibitoren für *Choristoneura murinana* Hbn. (Tannentriebwickler. Lepidoptera: Tortricidae) Anz. Schädlingskde., Pflanzenschutz, Umweltschutz 53:49-51.

Busck, A. 1915. Descriptions of new North American Microlepidoptera. Proc. Entomol. Soc. Wash. 17:79-94.

Campbell, I.M. 1953. Morphological differences between the pupae and the egg clusters of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. (Lepidoptera: Tortricidae). Can. Entomol. 85:134-136.

Campbell, I.M. 1958. A genetic study of factors determining fecundity in the Genus *Choristoneura* Lederer (Clem.) (Tortricidae). PhD Thesis, University of Toronto, Canada.

Campbell, I.M. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. Sexual isolation between three species. Can. Entomol. 99:482-486.

Canadian Forestry Service. 1939-1983. Annual reports of the Forest Insect (and Disease) Survey. Can. For. Serv. Ottawa.

Carolin, V.M. Jr.; Honing, F.F. 1972. Western spruce budworm. U.S. Dep. Agric., For. Ser., Forest Pest Leaflet 53. 8 p.

Carolin, V.M. 1980. Larval densities and trends of insect species associated with spruce budworms in buds and shoots in Oregon and Washington. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-273.

Castrovillo, P.J. 1982. Interspecific and intraspecific genetic comparisons of North American spruce budworms (*Choristoneura* spp.). PhD Thesis. Univ. of Idaho. 154 p.

Clancy, K.M.; Giese, R.L.; Benjamin, D.M. 1980. Predicting jack-pine budworm infestations in northwestern Wisconsin. Environ. Entomol. 9:743-751.

Clemens, B. 1865. North American Micro-Lepidoptera. Proc. Entomol. Soc. Philad. 5:139.

Cory, H.T.; Daterman, G.E.; Daves, G.D. Jr.; Sower, L.L.; Shepherd, R.F.; Sanders, C.J. 1982. Chemistry and field evaluation of the sex pheromone of the western spruce budworm. J. Chem. Ecol. 8:339-350.

Cox, C.E. 1953. Analysis of frequency distributions of adults and larvae of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. Can. Entomol. 85:136-141.

Cunningham, J.C.; Kaupp, W.J.; McPhee, J.R. 1983. A comparison of the pathogenicity of two baculoviruses to the spruce budworm and the western spruce budworm. Can. For. Serv., Ottawa. Res. Notes 3:9-10.

Dang, P.T. 1985. Key to adult males of conifer-feeding species of *Choristoneura* Lederer (Lepidoptera: Tortricidae) in Canada and Alaska. Can. Entomol. 117:1-5.

Daterman, G.E.; Cory, H.T.; Daves, G.D. Jr.; Stevens, R.E.; Fellin, D.G. (in press). Sex pheromones of three pine-feeding budworms of the *Choristoneura lambertiana* (Busck) complex in the western United States. Can. Entomol.

Daterman, G.E.; Cory, H.T.; Sower, L.L.; Daves, G.D. Jr. 1984. Sex pheromone of a conifer-feeding budworm, *Choristoneura retiniana*, Walsingham. J. Chem. Ecol. 10:153-160.

DeBoo, R.F.; Hildahl, V. 1968. Jack pine budworm in central Canada. Can. For. Serv., Ottawa. Liaison and Services Note. MS-L-4.

Diehl, S.R.; Bush, G.L. 1984. An evolutionary and applied perspective of insect biotypes. Ann. Rev. Entomol. 29:471-504.

Dobesberger, E.J.; Lim, K.P. Raske, A.G. 1983. Spruce budworm (Lepidoptera: Tortricidae) moth flight from New Brunswick to Newfoundland. Can. Entomol. 115:1641-1645.

Dolph, R.E. Jr. 1980. Budworm activity in Oregon and Washington 1947-1949. U.S. Dep. Agric., For. Serv., Pac. Northwest Region, R6, Portland, OR. FIDM-033-1980. 54 p.

Ennis, T.J. 1976. Sex chromatin and chromosome numbers in Lepidoptera. Can. J. Genet. Cytol. 18:119-130.

Eyre, F.H., Ed. 1980. Forest cover types of the United States and Canada. Society of American Foresters, Washington. 148 p.

Fellin, D.G.; Shearer, R.C.; Carlson, C.E. 1983. Western spruce budworm in the Northern Rocky Mountains. Western Wildlands 9:2-7.

Fellin, D.G. 1980. The western spruce budworm in the American Rocky Mountains. CANUSA Newsletter 8:1-3.

Ferrell, G.T. 1980. Growth of white firs defoliated by Modoc budworm in northeastern California. U.S. Dep. Agric., For. Serv., Pac. Southwest For. and Range Exp. Stn., Berkeley, CA. Res. Pap. PSW-153. 9 p.

Freeman, T.N. 1947a. A new generic assignment for *Archips fumiferana* (Clemens), the Spruce Budworm (Lepidoptera). Can. Entomol. 79:21.

Freeman, T.N. 1947b. The external anatomy of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. Entomol. 79:22-31.

Freeman, T.N. 1953. The spruce budworm, *Choristoneura fumiferana* (Clem.) and an allied new species on Pine (Lepidoptera: Tortricidae). Can. Entomol. 85:121-127.

Freeman, T.N. 1958. The Archipinae of North America (Lepidoptera: Tortricidae) Can. Entomol. 90:Supplement 7.

Freeman, T.N. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. I. Some new forms of *Choristoneura* allied to *C. fumiferana*. Can. Entomol. 99:449-455.

Gordon, A.G. 1984. Budworm! What about the forest?. Proc. 2nd Society of American Foresters Region VI Technical Conference, "Spruce-fir management and spruce budworm." Burlington, VT. 24-26 April 1984.

Graham, S.A. 1935. The spruce budworm on Michigan pine. U. of Mich. School of Forestry Bull. No. 6. 56 p.

Gray, T.G.; Slessor, K.N.; Grant, G.G.; Shepherd, R.F.; Holsten, E.H.; Tracey, A.S. 1984. Identification and field testing of pheromone components of *Choristoneura orae* (Lepidoptera: Tortricidae). Can. Entomol. 116:51-56.

Greenbank, D.O.; Schaefer, G.W.; Rainey, R.C. 1980. Spruce budworm moth flight and dispersal: new understanding from canopy observations, radar, and air craft. Mem. Entomol. Soc. Canada, No. 110.

Harris, J.W.E.; Alfaro, R.I.; Dawson, A.F.; Brown, R.G. 1985. The western spruce budworm in British Columbia 1909-1983. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Inf. Rep. BC-X-257.

Harvey, G.T. 1957. The occurrence and nature of diapause-free development in the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. J. Zool. 35:549-572.

Harvey, G.T. 1958. A relationship between photoperiod and cold storage treatment in the spruce budworm. Science 128:1205-6.

Harvey, G.T. 1961. Second diapause in spruce budworm from eastern Canada. Can. Entomol. 93:594-602.

Harvey, G.T. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. V. Second diapause as a species character. Can. Entomol. 99:486-503.

Harvey, G.T.; Stehr, G. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. III. Some characters of immature forms helpful in the identification of species. Can. Entomol. 99:464-481.

Harvey, G.T. 1974. Nutritional studies of eastern spruce budworm (Lepidoptera: Tortricidae) I. Soluble sugars. Can. Entomol. 106:353-365.

Harvey, G.T. 1977. Mean weight and rearing performance of successive egg clusters of eastern spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 109:487-496.

Harvey, G.T.; Roden, P.M. 1979. Special collection of coniferophagous *Choristoneura* species and hybrids at the Great Lakes Forest Research Centre, Sault Ste. Marie, Canada. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. Inf. Rep. O-X-293. 29 p + appendix.

Harvey, G.T. 1980. Sampling low density spruce budworm populations for isozyme analysis. Can. Entomol. 112:969-970.

Harvey, G.T. 1981. Variability in spruce budworm, *Choristoneura fumiferana*. Presented to Workshop on "Genetic variability of forest insect populations and implications for IPM". Page 58 *in* Proc. Thirty-second Annual Forest Insect Work Conference. U.S. Dep. Agric., For. Serv., Pac. Northwest Region., Portland, OR.

Harvey, G.T. 1982. Genetic variation in *Choristoneura fumiferana*. Presented to Joint Meeting of Entomological Societies of Ontario, Canada and America. Toronto, Canada. December 1982.

Harvey, G.T. 1983a. Isozyme analysis of *Choristoneura* species in eastern Canada. Presented to Annual Meeting of the Entomological Society of Ontario. Guelph, Ontario. October 1983.

Harvey, G.T. 1983b. A geographical cline in egg weights in *Choristoneura fumiferana* (Lepidoptera: Tortricidae) and its significance in population dynamics. Can. Entomol. 115:1103-1108.

Harvey, G.T. 1983c. Environmental and genetic effects on mean egg weight in spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 115:1109-1117.

Harvey, G.T. (in press). Egg weight as a factor in the overwintering survival of spruce budworm (Lepidoptera: Tortricidae) larvae. Can. Entomol.

Holsten, E.H. 1980. The status of spruce budworms in south-central Alaska, Chugach National Forest and adjacent lands. U.S. Dep. Agric., For. Serv., Anchorage, AK. Biological Evaluation R10-80-1. 15 p.

James, R.L. 1979. Jack pine decline in Nebraska National Forest. Distribution, insect and fungal associates. U.S. Dep. Agric., For. Serv., Rocky Mountain Region, Lakewood, CO. Biological Evaluation R2-79-4.

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of the western spruce budworm in the American Northern Rocky Mountain area from 1922 though 1971. U.S. Dep, Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rept. INT-20. 144 p.

Kettela, E.G. 1983. A cartographic history of spruce budworm defoliation 1967 to 1981 in eastern north america. Can. For. Serv., Ottawa, Ont. Inf. Rep. DPC-X-14.

Liebhold, A.M.; Volney, W.J.A. 1984a. Effect of temporal factors on reproductive isolation between *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae). Can. Entomol. 116:991-1005.

Liebhold, A.M.; Volney, W.J.A. 1984b. Effect of foliage proximity on attraction of *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae) to pheromone sources. J. Chem. Ecol. 10:217-227.

Liebhold, A.M.; Volney, W.J.A. 1985. Effects of attractant composition and release rate on attraction of male *Choristoneura retiniana, C. occidentalis* and *C. carnana* (Lepidoptera: Tortricidae). Can. Entomol. 117:447-457.

Liebhold, A.M.; Volney, W.J.A.; Waters, W.E. 1984. Evaluation of cross-attraction between sympatric *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae) populations in South-central Oregon. Can. Entomol. 116:827-840.

Little, E.E. Jr. 1971. Atlas of United States Trees. Vol. I. Conifers and important hardwoods. U.S. Dep. Agric., For. Serv., Washington, D.C. Misc. Publ. No. 1146.

Lorimer, N. 1979. Genetic causes of pest population outbreaks and crashes, Pages 50-54 *in* M.A. Hoy and J.J. McKelvey, Jr., Genetics in relation to insect management. The Rockefeller Foundation, New York.

Lorimer, N. 1982. Morphological variation by population, host, and sex in spruce budworm. Environ. Entomol. 11:493-496.

Lyon, R.L.; Richmond, C.E.; Robertson, J.L.; Lucas, B.A. 1972. Rearing diapause and diapause-free western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae) on an artificial diet. Can. Entomol. 104:417-426.

MacKay, M.R. 1953. The larvae of *Choristoneura fumiferana* (Clem.) and *C. pinus* Free. (Lepidoptera: Tortricidae). Can. Entomol. 85:128-134.

MacKay, M.R. 1962. Larvae of North American Tortricinae (Lepidoptera: Tortricidae). Can. Entomol. 93. Supplement 28.

May, B.; Leonard, D.E.; Vadas, R.L. 1977. Electrophoretic variation and sex linkage in spruce budworm. J. Heredity 68:355-359.

McGregor, M.D. 1970. Biological observations of the life history and habits of *Choristoneura lambertiana* (Lepidoptera: Tortricidae) on lodgepole pine in southeastern Idaho and western Montana. Can. Entomol. 102:1201-1208.

McKnight, M.E. 1968. A literature review of the spruce, western and 2-year-cycle budworms. U.S. Dep. Agric., For. Serv., Rocky Mt. For. and Range. Exp. Stn., Fort Collins, CO. Res. Pap. RM-44.

McMorran, A. 1972. Effects of some environmental factors on the occurrence of second diapause in laboratory-reared *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 104:1649-1653.

Oliver, C.G. 1979. Genetic differentiation and hybrid viability within and between some Lepidoptera species. Am. Nat. 114: 681-694.

Oliver, C.G. 1983. Disturbance of eclosion sequence in hybrid Lepidoptera. Can. Entomol. 115:1445-1452.

Obraztsov, N.S. 1962. New species and subspecies of North American Archipini, with notes on other species (Lepidoptera: Tortricidae). Am. Mus. Novit. 2101:1-26.

Powell, J.A. 1964. Biological and taxonomic studies on Tortricine moths, with special reference to the species in California. Univ. California Pub. Entomology. 32:317 p.

Powell, J.A. 1980. Nomenclature of nearctic conifer-feeding *Choristoneura* (Lepidoptera: Tortricidae): Historical review and present status. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range. Exp. Stn., Portland, OR. Gen. Tech. Rep. PNW-100. 17 p.

Powell, J.A.; DeBenedictis, J.A. 1982. Taxonomic relationships and pheromone isolations among western spruce budworm populations Canada/U.S. Spruce Budworms Program-West, Portland, OR. Final Report. 40 p.

Powell, J.A. 1983. Tortricoidea. *In* R.W. Hodges, T. Dominick, D.R. Davis, D.C. Ferguson, J.G. Franclemont, E.G. Monroe and J.A. Powell, eds. Check list of the Lepidoptera of North America north of Mexico. E.W. Classey Ltd. and the Wedge Entomological Research Foundation, London. 284 p.

Prentice, R.M., Ed. 1966. Forest Lepidoptera of Canada. Vol 4. Microlepidoptera. Dept. of Forestry, Ottawa. Publication 1142. 840 p.

Priesner, E.; Bogenschütz, H.; Arn, H. 1980. A sex attractant for the European fir budworm moth, *Choristoneura murinana*. Z. Naturforsch. 35c:390-398.

Robertson, J.L.; Gillette, N.L.; Lucas, B.A.; Russell, R.M.; Savin, N.E. 1978. Comparative toxicity of insecticides to *Choristoneura* species (Lepidoptera: Tortricidae). Can. Entomol. 110:399-406.

Robinson, C.T. 1869. Notes on American Tortricidae. Trans. Am. Entomol. Soc. 2:261-288.

Roeloffs, W.L.; Comeau, A. 1969. Sex pheromone specificity: taxonomic and evolutionary aspects in lepidoptera. Science 165:398-400.

Roeloffs, W.L.; Brown, R.L. 1982. Pheromones and evolutionary relationships of Tortricidae. Ann. Rev. Ecol. Syst. 12:395-422.

Rowe, J.S. 1972. Forest Regions of Canada. Can. For. Serv., Ottawa. Publ. No 1300. 172 p.

Sanders, C.J. 1971a. Sex pheromone specificity and taxonomy of budworm moths (*Choristoneura*). Science 171:911-913.

Sanders, C.J. 1971b. Daily activity patterns and sex pheromone specificity as sexual isolating mechanisms in two species of *Choristoneura* (Lepidoptera: Tortricidae). Can. Entomol. 103:498-502.

Sanders, C.J.; Daterman, G.E.; Shepherd, R.F.; Cerezke, H. 1974. Sex attractants for two species of western spruce budworm, *Choristoneura biennis* and *C. viridis* (Lepidoptera: Tortricidae). Can. Entomol. 106:157-159.

Sanders, C.J. 1975. Factors affecting adult emergence and mating behaviour of the eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 107:967-977.

Sanders, C.J.; Weatherston, J. 1976. Sex pheromone of the eastern spruce budworm (Lepidoptera: Tortricidae): optimal blend of trans- and cis-11-tetradecenal. Can. Entomol. 108:1285-1290.

Sanders: C.J.; Daterman, G.E.; Ennis, T.J. 1977. Sex pheromone responses of *Choristoneura* spp. and their hybrids (Lepidoptera: Tortricidae). Can. Entomol. 109:1203-1220.

Sanders, C.J. 1984. Sex pheromone of the spruce budworm (Lepidoptera: Tortricidae): Evidence for a missing component. Can. Entomol. 116:93-100.

Schmidt, F.H.; Young, C.L. 1971. Larval coloration in *Choristoneura* spp. (Lepidoptera: Tortricidae). Bile pigment in haemolymph. J. Insect. Physiol. 17:843-855.

Schmidt, F.H. 1977. Differences in thermal requirements for diapause termination in two western *Choristoneura* spp. (Lepidoptera: Tortricidae). Can. Entomol. 109:1469-1474.

Schmidt, F.H.; Lauer, W.L. 1977. Developmental polymorphism in *Choristoneura* spp. (Lepidoptera: Tortricidae). Ann. Entomol. Soc. Am. 70:112-118.

Shepherd, R.F. 1961. A comparison of the developmental rates of one- and two-year cycle spruce budworm. Can. Entomol. 93:764-771.

Shepherd, R.F.; Dolph, R.E. 1979. Spruce budworms in the Pacific Northwest. CANUSA Newsletter Number 6, September 1979.

Silk, P.J.; Tan, S.H.; Weisner, C.J.; Ross, R.J.; Lonergan, G.C. 1980. Sex pheromone chemistry of the eastern spruce budworm, *Choristoneura fumiferana*. Environ. Entomol. 9:640-644.

Silk, P.J.; Wiesner, C.J.; Tan, S.H.; Ross, R.J.; Grant, G.G. 1982. Sex pheromone chemistry of the western spruce budworm, *Choristoneura occidentalis* Free. J. Chem. Ecol. 8:351-362.

Silk, P.J.; Kuenen, L.P.S.; Tan, S.H.; Roelofs, W.L.; Sanders, C.J. 1985. Identification of sex pheromone components of the jack pine budworm, *Choristoneura pinus pinus* Freeman. J. Chem. Ecol. 11:159-167.

Smith, S.G. 1944. The reproduction of the nucleus. Sci. Agric. 24:491-509.

Smith, S.G. 1945. The diagnosis of sex by means of heteropycnosis. Sci. Agric. 25:566-571.

Smith, S.G. 1953. Reproductive isolation and the integrity of two sympatric species of *Choristoneura* (Lepidoptera: Tortricidae). Can. Entomol. 85:141-151.

Smith, S.G. 1954. A partial breakdown of temporal and ecological isolation between *Choristoneura* species (Lepidoptera: Tortricidae). Evolution 8:206-224.

Stark, R.W.; Borden, J.H. 1965. Life history of *Choristoneura lambertiana subretiniana* Obraztsov (Lepidoptera: Tortricidae) attacking lodgepole pine. Can. Entomol. 97:684-690.

Stehr, G. 1954. A laboratory method for rearing the spruce budworm, *Choristoneura fumiferana* (Clem.). Can. Entomol. 86:423-428.

Stehr, G. 1955. Brown female — A sex-linked and sex-limited character. J. Hered. 46:263-266.

Stehr, G. 1959. Hemolymph polymorphism in a moth and the nature of sex-controlled inheritance. Evolution 13:547-560.

Stehr, G. 1964. The determination of sex and polymorphism in microevolution. Can. Entomol. 96:418-428.

Stehr, G. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. II. Geographic distribution in accordance with forest regions. Can. Entomol. 99:456-463.

Stevens, R.E.; Borg, T.K.; Thatcher, T.O. 1977. Notes on a pine-feeding budworm, *Choristoneura lambertiana ponderosana* (Lepidoptera: Tortricidae), in the Colorado rockies. Can. Entomol. 109:1269-1274.

Stock, M.W.; Robertson, J.L. 1980. Inter- and intra-specific variation in selected *Choristoneura* species (Lepidoptera: Tortricidae): a toxicological and genetic survey. Can. Entomol. 112:1019-1027.

Stock, M.W.; Castrovillo, P.J. 1981. Genetic relationships among representative populations of five *Choristoneura* species: *C. occidentalis*, *C. retiniana*, *C. biennis*, *C. lambertiana*, and *C. fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 113:857-865.

Thomas, A.W. 1976. The effects of temperature on the emergence of second-instar spruce budworm larvae. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-60. 8 p.

Unger, L.S. 1974. Forest Insect and Disease Conditions. Yukon Territory 1974. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Inf. Rep. BC-X-117. 13 p.

Unger, L.S. 1983. Spruce budworms in British Columbia. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Pest Leaflet 31.

Van Sickle, G.A.; Fiddick, R.L.; Safranyik, L. 1981. Page 6 *in* T.E. Sterner and A.G. Davidson, eds. Forest Insect and Disease Conditions in Canada 1980. Can. For. Serv. Ottawa.

Van Sickle, G.A.; Wood, C.S. 1983. Page 10-11 *in* T.E. Sterner and A.G. Davidson, eds. Forest Insect and Disease Conditions in Canada 1982. Can. For. Serv., Ottawa.

Volney, W.J.A.; Liebhold, A.M.; Waters, W.E. 1983a. Effects of temperature, sex, and genetic background on coloration of *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in south-central Oregon. Can. Entomol. 115:1583-1596.

Volney, W.J.A.; Waters, W.E.; Akers, R.P.; Liebhold, A.M. 1983b. Variation in spring emergence patterns among western *Choristoneura spp.* (Lepidoptera: Tortricidae) populations in southern Oregon. Can. Entomol. 115:199-209.

Volney, W.J.A.; Liebhold, A.M.; Waters, W.E. 1984. Host associations, phenotypic variation, and mating compatability of *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae) populations in south-central Oregon. Can. Entomol. 116:813-826.

Walsingham, T. 1879. Illustrations of typical specimens of Lepidoptera Heterocera in the collections of the British Museum. Part IV. North American Tortricidae. British Museum, London. 84 p.

Webb, F.E.; Bean, J.L. 1967. Jack-pine budworm *Choristoneura pinus* Freeman. *In* A.G. Davidson and R.M. Prentice, eds. Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. Canada Dept. of Forestry and Rural Development, Ottawa. 248 p.

Wilhite, E.A.; Stock, M.W. 1983. Genetic variation among western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae) outbreaks in Idaho and Montana. Can. Entomol. 115:41-54.

The Ecology of the Eastern Spruce Budworm: A Review and Discussion

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Spruce budworm outbreaks are associated with fluctuations in forest composition and age. Since the beginning of the 20th century, the frequency and extent of outbreaks have increased in eastern North America because of modifications in forest composition resulting from man's actions. Effects of weather and biocontrol factors on insect populations are reviewed. Where and how outbreaks originate and develop are also discussed. Some important aspects of the epidemiology of this insect still need to be clarified.

Les invasions de la tordeuse des bourgeons de l'épinette sont reliées aux variations périodiques de la composition et de l'âge des forêts. Depuis le début du vingtième siècle, la fréquence et l'étendue des invasions augmentent dans l'est de l'Amérique du Nord; cette situation est due aux interventions de l'homme en milieu forestier. Les effets du climat et des facteurs naturels de lutte sur les populations de l'insecte sont examinés. Les lieux d'origine et les raisons de la progression des invasions font également l'objet de discussions. D'importants aspects de l'épidémiologie de cet insecte sont encore mal connus et devront être clarifiés.

Introduction

The relationship of an organism with its environment often is very complex. This is certainly true for the eastern spruce budworm (*Choristoneura fumiferana* (Clem.)). Outbreaks of this native insect recur periodically and are a natural phenomenon, the result of the co-evolution of a plant-insect system. Populations of this insect can remain at an endemic level for long periods; in the past, intervals between outbreaks have varied from 30 to over 100 years. When epidemics develop they usually cover extensive areas and last several years. Biotic and abiotic factors that affect budworm populations and that can influence short and long-term population fluctuations include parasitoids, predators, disease, food supply, and weather. Insect numbers probably vary on a short-term basis during periods when populations are at endemic levels, but this remains to be determined. However, it is well documented that short-term population fluctuations take place during the course of epidemics. These fluctuations can have important consequences since they influence the rate of tree mortality thereby affecting control programs, presalvage, and salvage operations. These short-term population fluctuations usually cannot be predicted and are often caused by weather or by unknown factors (Blais 1983c). Of greater significance than the short-term population fluctuations are the long-term fluctuations associated with the recurrence of budworm epidemics. The determination of factors responsible for budworm epidemics is crucial to the forest manager. The manipulation of these factors, or at least some of them, could possibly lead to a reduction in the frequency of outbreaks and their effect on the forest. A complete review of the literature on the ecology of this insect would be voluminous; in this presentation I will briefly discuss some of the more important known, as well as some less well documented or more controversial aspects of the subject.

Forest-Insect Relationship

Studies on the epidemiology of this insect have been pursued for the past 60 years. Most of those who have conducted such studies believe that outbreaks are part of the dynamics of forests where balsam fir (*Abies balsamea* (L.) Mill.) is an important constituent. According to Rowe (1972) the geographical distribution of fir in eastern North America is very extensive and includes most of the Great Lakes – St. Lawrence Forest Region, the southern section of the Boreal Forest Region, and most of the Acadian Forest Region. Although Rowe's forest classification applies to Canada, the Great Lakes – St. Lawrence Forest Region extends in the United States to New England and the Lake States. Tothill (1919) and Swaine and Craighead (1924) were the first to suggest that budworm outbreaks were associated with the presence of extensive stands where mature fir occurs. Since then, many investigators working in several outbreaks in several regions in both Canada and the United States have come to the same conclusion.

Stands where mature fir is present offer conditions favorable to the budworm. One condition appears to be the frequent and heavy production of flowers by mature trees. Balsam fir is considered as attaining maturity at 60 years. From 60 years on, fir trees bear frequent and heavy flower crops, but it is significant that flower production can be abundant in trees from about the age of 45. The influence of staminate flowers on budworm was first investigated in 1945 by Bess (1946) in western Quebec. Studies on the relationship of the budworm to the flowering condition of fir were then conducted in Ontario by Blais (1952) between 1946 and 1950, and in New Brunswick by Greenbank (1963b) during the early 1950s. Field and laboratory studies by these last two investigators carried out during 10 years showed that: 1) budworm populations were more abundant on flowering than on nonflowering trees; 2) first instar larvae (L_1) prefer to overwinter in bracts remaining from old staminate flowers, and that they settle more rapidly in flower bracts than in other sites; 3) second instar (L_2) larvae upon emerging from hibernacula in the spring establish feeding sites in swollen flower buds in preference to mining needles of old foliage or unopened vegetative buds; 4) larvae feeding on pollen have an advantage in their development ranging from 3 to 7 days. It has been established that about 60 to 70 percent mortality of small larvae is associated with fall and spring dispersal (Miller 1958). Blais (1952) concluded that higher populations on mature fir were due in part to reduced losses resulting from reduced dispersal on flowering trees. Greenbank (1963b), on the other hand, believed that the key to the maturity factor was due to the favorable eco-climates provided by the more open-grown mature stands in comparison to the cooler, more humid climates of dense, young stands.

Because flower production is interrupted through the destruction of shoot growth by defoliation, the role played by the presence of flowers is more readily discernable during the initial phase of an outbreak (Blais 1952). However, the importance of staminate flowers on the survival of budworm populations can also be apparent during more advanced stages of an outbreak. It is significant that the spectacular spread of the outbreak in Quebec from 1973 to 1974 coincided with an unusually heavy production of flowers on fir and spruces in 1974. In 1973, the outbreak occupied about one-third of susceptible forests in the province; in 1974, the outbreak had spread to most of the susceptible stands and moderate to severe defoliation occurred over 320 000 km^2 (830,000 mi.^{2}) (Martineau et al. 1976). Another year of unusually high flower production on fir and spruces occurred in 1982 in Quebec and in the Maritimes, and this again resulted in increased survival of the insect as indicated by defoliation and egg-mass surveys (Benoit et al. 1983; Kettela 1982).

Budworm outbreaks usually result in the destruction of very large quantities of fir, and to a lesser extent white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubra* Sarg.), and black spruce (*Picea mariana* (Mill.) B.S.P.). Losses on a regional basis and for different outbreaks have been reported by several investigators (Swaine and Craighead 1924; Graham and Orr 1940; Turner 1952; Elliott 1960; Blais 1964a, 1981a; Mog et al. 1982; Howse et al. 1982; Beaulieu and Hardy 1982; Brann et al. 1983; Kucera and Taylor 1983). These losses amounted to large proportions of the fir in each region and resulted in a considerable reduction in the merchantable volume of this tree species, often reaching between 80 and 90 percent. In his review and analysis of available information from the literature on the vulnerability of spruce-fir stands during uncontrolled spruce budworm outbreaks, MacLean (1980) concluded that mortality in mature fir stands approaches 100 percent. Generally, reduction in food supply is responsible for the collapse of outbreaks.

Although the return of budworm populations to the endemic level is usually associated with food depletion, there are a few instances where outbreaks have collapsed before the destruction of large volumes of fir. Of the 31 recorded outbreaks during the past 200 to 300 years for 9 different regions in eastern Canada, only 5 outbreaks did not result in extensive tree mortality (Blais 1983b). Of these, the collapse in 1958 of the outbreak in the Gaspé Peninsula and in northern New Brunswick is best documented (Blais and Martineau 1960). However, this outbreak would have caused extensive tree mortality had it not been for 7 consecutive years of aerial application of DDT (Webb et al. 1961). For the Lower St. Lawrence and the Gaspé Peninsula, which is just part of the outbreak area, the loss averted through treatment has been estimated at 47 million m^3 (13 million cords) (Blais and Martineau 1960). Using data on budworm population studies obtained during the past 30 years in New Brunswick, Royama (1984) concludes that food shortage is not a universal cause of population decline. This is a logical conclusion in the light of existing conditions in New Brunswick. These conditions, however, are exceptional and are probably the result of a disruption in the insect-forest relationship brought about through 30 years of continuous treatment with insecticides that kept a major portion of the forest alive.

The other known outbreaks that occurred on a regional scale in Canada and that resulted in light tree mortality took place in the Laurentian Reserve in Quebec in 1802 and 1832 (Blais 1965b), in the Gaspé Peninsula in 1912 (Blais 1961), and on Quebec's North Shore in 1948 (Brown 1970; Blais 1983a). It is noteworthy that the prevailing climate in all these regions is marginal for budworm.

At the endemic level, budworm populations are extremely low. Greenbank (1963a) reports that before the outbreak that began in 1947 in New Brunswick, only 10 larvae were found in over 1000 collections made each summer between 1939 and 1944. During studies on field spruce insects in the Gaspé Peninsula in 1959, one year after the collapse of the 1947-1958 outbreak, 140 spruce budworms were collected, 125 in the early larval stage, 9 in the sixth larval instar and 6 in the pupal stage. This was the result of continued searching for all species of insect defoliators from white spruce foliage by four workers over a period of 2 months (Blais 1959b). At the time of maximum level of feeding larvae, spruce budworm was fifth in order of abundance of species of defoliators recovered (McLeod and Blais 1961). In the mid-1960s, all regions in the province of Quebec were free of budworm outbreaks, and in 1965, only two specimens of the spruce budworm were collected by the Forest Insect Survey of the Department of Forestry and Rural Development. In studies on endemic budworm populations conducted during 1961 and 1962 in northwestern Ontario, Fye (1963) found that populations ranged between 0 and 0.3 per 1 m^2 of balsam fir foliage, even less were found on white spruce. Miller and Renault (1976) who studied endemic budworm populations on balsam fir in northern New Brunswick between 1960 and 1971 estimated feeding larvae at 3-5 per middle-aged fir tree, and pupae at 1 per 100 mid-crown branches.

Although outbreaks may bring about some local changes in species composition, there is no indication that they modify species composition on a widespread basis (Halliday and Brown 1943; Blais 1959a; Baskerville 1975; MacLean 1984). The forest floor in mature and even in immature fir stands is usually occupied by abundant regeneration of fir, and this gives rise to the succeeding forest in killed stands. It is only with the advent of a new generation of mature or near mature fir trees over widespread areas that conditions once again become propitious to the development of another outbreak. Thus, outbreaks result in oscillations in the age-class distribution of fir.

In recent times, some observers have implied that balsam fir may be less "preferred" by the insect than red spruce or white spruce even though fir succombs sooner to budworm attack (Hardy 1979; Webb and Irving 1983). Evidence indicates this premise is unlikely. Red spruce is a species with a limited distribution (Rowe 1972) and it cannot have any influence on the dynamics of budworm populations over the greater part of the area subject to attack in eastern North America. White spruce occurs in all areas where fir is present, but in much smaller numbers than fir; for instance white spruce and fir comprise 5 percent and 22 percent respectively of the total volume of all tree species in Quebec (Quebec Department of Lands and Forests 1975). Important amounts of white spruce are occasionally killed by budworm although in much fewer numbers than fir (Turner 1952; Elliot 1960; Blais 1981a). Other records indicate that mortality of white spruce can be negligible even when mortality of fir is very high (Swaine and Craighead 1924; Blais 1981a). This would indicate that budworm outbreaks are generally not associated with oscillations in volumes of white spruce as they are with fir. However, this should not be construed as an indication that white spruce is not an important accessory in population dynamics of this insect.

A case history of budworm outbreaks in the Gaspé Peninsula sheds some light on the possible relationship of white spruce to such outbreaks. In this region, there were no outbreaks during the 19th century, while three occurred in the 20th century (Blais 1961). The first of these began about 1912; it was a light infestation and was mostly confined to the southwestern part of the region. Following this outbreak, severe infestations of the European spruce sawfly (*Diprion hercyniae* (Htg.)) and the eastern spruce beetle (*Dendroctonus rufipennis* Kby.) occurred between 1930 and 1938 resulting in the mortality of an estimated 65 percent of the white spruce (Gobeil 1938). Ten years following the decimation of the white spruce, another budworm outbreak developed in the Gaspé Peninsula which was considerably more severe and widespread than the 1912 outbreak (Blais and Martineau 1960; Blais 1961), even though white spruce was much less abundant than at the time of the preceding outbreak.

Outbreak Cycles

The history of spruce budworm outbreaks for periods varying between 200 and 300 years has been determined through radial-growth studies on old white spruce trees for nine regions encompassing most of the territory subject to budworm attack in eastern Canada (Blais 1954, 1961, 1964b, 1965b, 1968, 1981b, 1983a; Turner 1952). These studies indicate outbreaks have occurred more frequently in the 20th century than previously (Blais 1983b). Regionally, 23 outbreaks took place in the past 80 years compared to 9 in the preceding 100 years. Earlier infestations were restricted to specific regions, but in the 20th century they have coalesced and increased in area; the outbreaks of 1910, 1940, and 1970 having covered 10, 25, and 55 million ha (25, 62, and 136 million acres) respectively. Reasons for the increase in frequency, extent, and severity appear to be attributable to changes caused by man in the forest ecosystem. Harvesting of pulpwood stands, fire protection, and pesticides used against budworm favor spruce–fir stands, rendering the forest more prone to budworm attack. This becomes more evident when the history of outbreaks in western Ontario and on the North Shore in eastern Quebec is compared with that in the central portion of the territory. In western Ontario and eastern Quebec, forest exploitation on a large scale and fire protection began recently, and the effect of such practices are only beginning to be felt. In these two regions, intervals between outbreaks have been long, averaging about 100 years, and their frequency of occurrence, until very recently, has remained unchanged. In the central portion of the territory, outbreak-intervals lasting between 75 and 100 years were common prior to the 20th century. It is mostly since then that man's actions have modified the forest composition with the result that budworm infestations are more widespread and outbreak intervals have been reduced to about 25 years in this sector (Blais 1983b).

A new theory suggests budworm populations do not remain at the endemic level but that they reach a trough and increase again without hesitation resulting in a 30-40 year oscillation (Royama 1984). It is difficult to accept this theory considering some shorter intervals between outbreaks during the 20th century and especially much longer ones prior to this century (Blais 1983b).

Weather

There is considerable evidence to show that warm and dry conditions favor spruce budworm survival. Wellington et al. (1950) determined that the beginning of several budworm outbreaks had been preceded by a period of 3 or 4 years of early summer drought. Studies conducted in various regions by Greenbank (1956), Pilon and Blais (1961), and Ives (1974) have shown a similar relationship. Hardy et al. (1983) also suggested that outbreaks generally arise in zones where the climate is relatively warm and dry. Heavy production of flowers is often brought about by stress caused by drought conditions. Greenbank (1963b) observed that the incidence of flowering in fir is increased the year following inordinately sunny and dry summers. The importance of staminate flowers in providing conditions favorable to the insect has already been briefly discussed; it could be that it is the combined effect of weather and flowers that contributes to the initiation of budworm outbreaks.

If weather is a factor in releasing budworm populations, it can also play a part in population fluctuations during infestations and in the duration of infestations. In regions where the climate is relatively warm and dry, all known outbreaks terminated as a result of food depletion except one in eastern Quebec and northern New Brunswick (Blais 1983b). In this instance, as mentioned earlier, the insect-forest relationship had been disrupted through 7 years (1952-58) of treatment with DDT. Of the other known outbreaks that ended through causes other than food depletion; two took place in the 19th century in the Laurentian Reserve, one in the early 20th century in the Gaspé Peninsula, and one in the mid-20th century on Quebec's North Shore (Blais 1983b). The highest elevations (reaching above 800 m [3,000 ft]) in the sector subjected to budworm attack in eastern Canada occur in the Laurentian Reserve and in the Gaspé Peninsula. This results in a climate that is generally wet and cool with precipitation averaging 152 cm (60 in) and a frost-free period of about 2 months. The climate on the North Shore is also generally wet and cool because of the latitude and the proximity of the Gulf of St. Lawrence. It should be kept in mind that in each of these regions although some outbreaks were of short duration, others persisted long enough to cause extensive tree mortality. Another phenomenon that lends support to the premise that climate in these regions is marginal for budworm is the occasional abrupt and drastic reductions in populations that may last a few years before populations return to high levels. This occurred in the Laurentian Reserve during the 1946 outbreak (Blais 1964a) and the 1970 outbreak (Blais 1980), and on the North Shore during the 1970 outbreak (Blais 1983a). Balsam fir grows best in regions with a cool and wet climate. It is significant that areas with the highest fir content and therefore most favorable for the budworm's food supply, are those where climate is marginal for the insect. This explains why in these areas budworm outbreaks can follow an erratic course. There is only one known instance where budworm populations collapsed temporarily in the course of an outbreak in a region with a more temperate climate; I am referring to the situation that prevailed in the St. Maurice River watershed in Quebec in the late 1970s and that will be discussed under the section dealing with parasitoids.

Several studies, including those by Morris (1963), have been conducted to determine overwintering mortality of budworm. Almost without exception these studies indicate that mortality seldom exceeds 15 percent. This is corroborated by sampling of overwintering populations for a period of over 10 years by members of the Conservation Branch of the Quebec Department of Energy and Resources as indicated in their annual reports connected with control programs against the spruce budworm. The insect appears to be well adapted to the extremes of winters in eastern North America.

Emergence from the hibernacula in the spring and from the eggs in mid-summer takes place over relatively short periods of time, and these two stages in the life-history of the insect may be critical and may play an important role in the rate of survival. Laboratory experiments and historical data tend to show that prolonged rain and freezing temperatures during and shortly after emergence in the spring may sometimes have a profound impact on outbreak development (Lucuik 1984). It is conceivable that prolonged wet weather could also result in high mortality during the two-week period of emergence from the eggs in July.

Dispersal

Some dispersal takes place during all the active stages of the budworm. Throughout the course of the feeding stage, dispersal is limited to within and between trees within a stand. During emergence from the hibernacula and from the eggs, dispersal of the small larvae is more widespread and can result in the extension of outbreaks. The distance small larvae can be transported by air currents is not well known but is probably limited to a few kilometres. Furthermore, the extent of dispersal of small larvae can vary considerably between years depending on weather conditions and on the type and quantity of food supply (Blais 1952). Dispersal during these stages can result in considerable loss of population (Miller 1958) and this in turn could play an important role in the dynamics of the spruce budworm.

Moth dispersal is probably the most significant form of dispersal of this insect, and is the form that has been the most studied. A research program in New Brunswick coordinating the use of radar, specifically instrumented aircraft, and observations from platforms extending above the forest canopy has established the massive scale and regularity of evening take-off and flights by spruce budworm moths, and of subsequent nocturnal dispersal at levels high above the ground (Greenbank et al. 1980). A high proportion of moths collected in this study during emigration, displacement, and immigration were egg-carrying females. This integrated research program has provided new data for better evaluation of the significance of moth dispersal in the initiation and spread of infestations. It is now known that large numbers of moths can disperse and invade regions as distant as 600 km (373 mi.) from their point of origin (Dobesberger et al. 1983).

The general progress of outbreaks from west to east indicates that spread is attributable, at least in part, to the dispersal of moths by prevailing westerly winds. Furthermore, an implication of nonrandom moth movement is that in the early stages of development of an outbreak, moths emigrating from large areas of low population density may be concentrated sufficiently on immigration to trigger an outbreak through the budworm population in the area of deposition to rise above the level controlled by natural enemies (Morris et al. 1958; Clark et al. 1978). There remains much to be learned in the role played by moth dispersal in the initiation, maintenance, and spread of spruce budworm outbreaks.

Biocontrol and Unknown Factors

The biocontrol factors operating against budworm survival are disease microorganisms, predators, and parasitoids. There is no evidence in the literature that either fungi, viruses, bacteria, or microsporidia have caused sufficient mortality during budworm outbreaks to be classified as even mildly epizootic (Neilson 1963). Likewise, predators do not appear to seriously affect this insect during the epidemic phase. Of the biocontrol factors, the action of parasitoids appears to be the most important and has been the most studied. Since 1943 to the present, investigations on the action of parasitoids have been conducted in several regions in both Canada and the United States. Approximately 90 species of entomophagous parasites have been recovered from spruce budworm, but only about 15 species are common (McGugan and Blais 1959; Miller 1963). Of these, just two: *Apanteles fumiferanae* Vier., and *Glypta fumiferanae* (Vier.) have their life cycles synchronized with the host. The others require alternate hosts, hence their limitation in controlling budworm populations at outbreak levels. During periods of high host density *Apanteles* and *Glypta* are the most common parasitoids, however, together they usually kill less than 20 percent of the larvae. It is surprising that their numbers in relation to those of the host do not increase during the course of an outbreak; some unknown factor prevents them from doing so. There is only one instance where records show a high degree of mortality (about 60 percent of the larval population) caused by the combined action of *Apanteles* and *Glypta*; this occurred in central Quebec in 1975 (McLeod 1977; Bonneau and Bordeleau 1976). This situation might have contributed to the drastic reduction in host density in this region the following year. Host populations remained low until 1982 when they returned to high levels.

When budworm populations are depressed below a certain critical level as a result of food depletion or through other causes, percentage mortality through parasitism can increase considerably as has been repeatedly observed (Dowden et al. 1950; Jaynes and Drooz 1952; McGugan and Blais 1959; Blais 1960, 1965a; Miller 1963). This results from an increase in the action of parasite species that are scarce when host populations are high. *Meteorus trachynotus* Vier has been frequently recovered and several other species have appeared sporadically. When budworm populations are returning to endemic levels, the parasite complex and the relative abundance of each parasite species is determined by the presence and the relative abundance of alternate hosts.

Attempts to study the influence of parasitoids during the endemic population phase in Ontario, Quebec, and New Brunswick have met with only moderate success especially for the late-larval and pupal stages due to the extreme scarcity of the host population (Blais 1959b; Fye 1963; Miller and Renault 1976).

Probably parasites exert some compensatory mortality on budworm populations during the endemic phase. With increases in the host density, parasitoids kill only a moderate proportion of the population. Generally, it is only during the final year of an outbreak that the action of parasites shows a pronounced increase. This increase is a symptom of the collapse rather than a cause of it.

Royama (1984) rejects the commonly accepted theory of outbreaks based on the dichotomy of endemic and epidemic equilibrium states. He considers that a basic oscillatory trend with an average of 35 years is determined by the combined action of several factors that include parasitoids, disease, and most important, a complex of unknown causes which he terms "the fifth agent." The premise is based on data obtained by Neilson (1963) to determine the incidence of larval mortality attributable to disease during the period immediately preceding and including population decline in New Brunswick between 1954 and 1958. Larvae were collected from a single plot on a weekly basis and reared in a laboratory; a large number of larvae died with no clear symptoms during the rearings. Many budworm larvae and pupae die from undetermined causes in rearings as has repeatedly been observed during studies since the 1940s. At least some of this mortality is attributable to handling as this insect is not easily manipulated. The extent of mortality through undetermined causes in the field is not known and is most difficult to measure. The phenomenon of population decline and final collapse during the last 3 years of the 1947-58 outbreak in northern New Brunswick also took place in the adjacent region in Quebec. Between 1954 and 1958 an average of 4500 budworm larvae were obtained each year from 7 to 11 scattered localities in this region in Quebec and were reared for parasite investigations (Blais 1960). Mortality of small larvae due to causes other than parasitoids, and these were mostly unknown causes, amounted to 22, 19, 25, 26, and 25 percent, and of large larvae to 17, 13, 19, 24, and 12 percent for 1954, 1955, 1956, 1957, and 1958 respectively. There was no apparent increase in the rate of mortality due to undetermined factors during these years. The degree of mortality due to unknown causes observed in Quebec is close to that I observed during the course of 10 years of studies during the peak of the declining phase of various outbreaks in Ontario and Quebec (McGugan and Blais 1959; Blais 1965a). Neilson (1963) recognizes the inadvisability of using data on disease from one plot to represent conditions over a large area (Morris 1963, p. 280). Certainly more evidence is required to substantiate Royama's theory.

Origin of Outbreaks

Because budworm populations are so low at the endemic level, population release can occur at least 3 to 4 years before defoliation becomes apparent. Until now, the means to detect the initial rise in insect numbers has not been available. Whether outbreaks begin in discrete epicenters, or whether populations increase more or less simultaneously over fairly large areas has not yet been established. It is possible that both phenomena take place. The rapidity with which the size of certain outbreaks has increased would indicate that, at least at certain times, population increase takes place over large areas rather than as a result of spread from discrete centers. Data on the progress of budworm outbreaks in eastern Canada between 1969 and 1975 support this premise. Within a period of 6 years, three relatively small outbreak centers, one in eastern Ontario, one in western Quebec, and one in New Brunswick spread and amalgamated to encompass nearly all susceptible stands in eastern Canada from central Ontario to Newfoundland. The areas under budworm attack covered 1, 10, 22, and 56 million ha (3, 25, 54, and 138 million acres) in 1969, 1971, 1973, and 1975 respectively (Kettela 1983). Although moths can be transported long distances by air currents (Greenbank et al. 1980), it is questionable whether this rapid expansion could have resulted solely through moth dispersal. Royama (1984) postulates that dispersal acts like a fertilizer to stimulate the seed of an outbreak (survival of local larvae) that has already started growing in every locality. This premise probably reflects reality.

If outbreaks did stem from discrete epicenters, a very elaborate system of detection would be required to discover these focal points. This in itself would be no mean feat considering the vastness and difficulty of accessibility of the areas susceptible to attack. It should be kept in mind that defoliation could not be used as a criterion to establish the boundaries of an epicenter. Insect populations could be on the rise over a much larger area than that delimited by defoliation; a small area of defoliation might be to the total area of infestation what the visible point of an iceberg is to its total mass.

On the basis of studies conducted in Quebec during the recent outbreak, it has been suggested that outbreaks arise in mixed stands in the Great Lakes – St. Lawrence Forest Region rather than in spruce–fir stands in the Boreal Forest Region. From this it is implied that extensive stands of fir are not necessarily a prerequisite for the initiation of outbreaks (Hamel 1978; Hardy 1979; Hardy et al. 1983). It is further postulated that budworm populations generally do not maintain themselves at high levels in this so-called zone of population release where they cause little damage, but spread to the more vulnerable stands farther north. Severe and widespread damage has been caused by budworm, at least since the beginning of the 20th century, to stands within the Great Lakes – St. Lawrence Forest Region. Treatment of stands within this region in Canada and the United States suggests that practitioners have recognized this fact. Furthermore, fir and white spruce are important constituents of forests in the Great Lakes – St. Lawrence Forest Region (Halliday 1937; Rowe 1972). A rating of the vulnerability of forests to budworm attack on a forest management unit basis was determined for Quebec

(Blais and Archambault 1982). Merchantable volume of fir and white spruce, and maturity of fir based on recent forest inventories were the main criteria that served to determine the ratings. The merchantable volume of fir and white spruce differed little between management units in the Great Lakes – St. Lawrence Forest Region and those immediately to the north in the Boreal Forest Region. Of the 13 management units that cover most of the Great Lakes – St. Lawrence Forest Region in Quebec, 11 were classified as being highly vulnerable to budworm; it comes as no surprise that outbreaks can originate here. Vast continuous stands of fir are not necessarily a characteristic of the boreal forest. They are rather an exception and occur in areas of high precipitation such as the Laurentian Reserve, the Gaspé Peninsula, and the highlands of Cape Breton Island (Halliday and Brown 1943). Elsewhere, spruce–fir stands are more discontinuous and much of the fir occurs in mixed stands throughout its range.

Although outbreaks can start in the Great Lakes – St. Lawrence Forest Region, it is erroneous to believe this is always the case. To suggest, as has been done (Quebec Government Office of Public Hearings on the Environment 1983), that managers who aim at rendering the forest more resistant to budworm should concentrate their efforts in this zone is therefore ill advised. Several records show that outbreaks have originated well within the boreal forest. The so-called Lake Nipigon and Lac Seul infestations that occurred in the early 1940s in western Ontario are good examples (Blais 1954; McGugan and Blais 1959; Elliott 1960). The first of these originated along the southwest shore of Lake Nipigon. This outbreak lasted over a decade and remained confined to the boreal forest (Brown 1970). The Lac Seul outbreak had two areas of origin, one near Sioux Lookout and the other approximately 100 km (60 mi.) west of Sioux Lookout. It took 12 years for this outbreak to spread southward and reach the Great Lakes – St. Lawrence Forest Region (Brown 1970). Forest stands in these areas of origin are very typical of the boreal forest and in no way resemble the Laurentian and the yellow birch–maple associations related to the epicenters of the recent outbreak in Quebec (Hardy et al. 1983). Studies on the history of past budworm infestations in the Lac Seul area revealed that a severe and prolonged outbreak occurred in the 1860s; the data indicate this outbreak also originated near Sioux Lookout (Blais 1954). Additional evidence that outbreaks can originate in the boreal forest can be gained from more recent records. In the 1969 Annual Report of the Forest Insect and Disease Survey, under the section dealing with the Chapleau – Onaping Lake region in Ontario it is mentioned: "In northeastern Ontario an outbreak which first became evident as a large area of light defoliation in 1967 now comprises numerous areas of moderate to severe defoliation totalling 2,800 square miles" (Sippell et al. 1970). More recently, a new infestation covering 60 700 ha (239 mi.^{2}) was detected in 1980, immediately southwest of Lake Nipigon (Howse et al. 1982). This new outbreak is very close to the area of origin of the Lake Nipigon outbreak that began 40 years earlier and referred to above.

Management practices aimed at reducing the frequency of occurrence and the impact of future outbreaks should be applied in the Boreal Forest Region as well as in the Great Lakes – St. Lawrence Region. In both regions, efforts should not be confined to spruce–fir stands but should also include mixed stands. Yang and Fry (1981) conclude that current logging practices in the boreal mixedwood forest are bringing about "a tremendous influx of balsam fir seedlings... which implies even greater representation of this species in future rotations in the absence of silvicultural treatment favoring other species."

Discussion and Conclusions

An understanding of the epidemiology and of the population dynamics of the spruce budworm is essential to any short- or long-term measures aimed at reducing the socio-economic consequences of future outbreaks of this insect. In this paper, I have attempted to briefly review the major aspects of what information we possess on this subject. This information, although considerable, is far from complete, and some of it is controversial. This should be of major concern to all who are preoccupied with the budworm problem. Why have we not made better progress in this important field of research? The reasons are many; for one, the number of workers that have studied this aspect, especially during the past 20 years has been far too few, and for another, the problem is very complex because outbreaks occur at long intervals and budworm populations at the endemic level are so low. The initial release of populations can occur 3 to 4 years before defoliation becomes apparent, and until recently the means to detect an initial rise in insect numbers was not available. The use of pheromone traps may assist in overcoming this drawback.

The area prone to budworm outbreaks in eastern North America is vast with variations in climate, forest composition, and where actions by man have differed. This is reflected in variations in the ecology of the budworm between sectors. In the western sector of the area subject to budworm attack in eastern North America, balsam fir is a much less important constituent of the forest while the climate during the growing season is warmer and drier than in the eastern sector. Management aimed at reducing the fir content of the forest has for many years, especially in the eastern sector, been considered as a possible long-term measure to lessen the effect of future outbreaks. This step, however, would require further scrutiny before attempts are made to implement it. According to Halliday and Brown (1943), population intensity of fir is less than 10 percent in the western sector, while it is about 30 percent in the eastern sector. Notwithstanding the low fir population, the western sector is subject to periodic attacks by the budworm. Therefore, is it realistic to suggest that reducing the fir content of forests in the east might make them less vulnerable to future attacks by the budworm? The application of such a measure, in spite of the inherent difficulties, deserves serious consideration. The point I wish to make is that studying conditions in the western sector could provide valuable information on the possibility of applying certain measures aimed at rendering forests in the east more resistant to budworm. This is just one instance where lessons gained from one region could contribute to a better understanding of a situation in another region.

Because the behavior of budworm outbreaks between regions, and between successive outbreaks within a region can vary considerably, conclusions derived from observations conducted on a regional basis during the course of one outbreak do not necessarily apply at large. It is dangerous to generalize on studies limited in time and place, and in recent years, this has led to some controversies on budworm epidemiology. To understand the behavior of budworm outbreaks and their effect on the forest, studies must be conducted in many regions as well as during the course of successive outbreaks within a region. Similarities and differences between regions and between outbreaks must be studied to gain knowledge on the basic principles associated with the many facets of the ecology of the budworm. These studies, of necessity, are long term and most certainly cannot be performed on a contract basis. They could be undertaken by individuals who are generalists by attribute and who combine knowledge in entomology and especially in forest ecology. However, these investigations would best be undertaken by multidisciplinary groups not unlike the one that studied the dynamics of epidemic spruce budworm populations during the period 1945-1959 in northern New Brunswick. Such a group, or better still groups, would not necessarily stress the analysis of survival and reproduction of the insect, as important as these studies might be, but rather concentrate on the forest–insect interelationships, and this, on a broad rather than on a regional basis. It is a reflection of our times that, at least in Canada, such a program would have been easier to accomplish 20 years ago, when personnel and funds were more readily available, than today.

Several important aspects of the epidemiology of this insect still need to be clarified. One of these is where and how outbreaks arise. It is likely that conditions propitious to the release of populations occur more or less simultaneously over large areas, but this has yet to be demonstrated. If outbreaks arise from discrete epicenters, what is the size of such epicenters, and in what types of stands do they occur? If epicenters exist, if they are restricted in area, and if they can be detected in time, it is conceivable that control measures could be applied to prevent their extension. At this stage, however, this can only be considered as a remote possibility.

The spread of outbreaks, often at a very fast rate is another aspect of the epidemiology that is not well understood. What role is played by the dispersal of L_1 and L_2 larvae, and especially moths? To what extent if any, is the spread of infestations attributable to successive increases in local populations? How do forest characteristics affect the rate of diffusion of epidemics?

Effects of weather during the various active stages of the insect are not well understood because they have not been sufficiently studied. This applies particularily to the periods of emergence from the hibernacula in the spring and from the eggs in July, and the adult stage.

Although much remains to be learned, we, nevertheless, possess a considerable amount of information about the budworm itself. It is the insect–forest relationship that still holds many mysteries. This relationship is the most fascinating aspect of the budworm problem and it is only when it is better understood, that a solution to the problem may be found.

Literature Cited

Baskerville, 1975. Spruce budworm: super silviculturist. For. Chron. 51:138-140.

Beaulieu, J.; Hardy, Y. 1982. Mortalité du sapin baumier défolié par la tordeuse des bourgeons de l'épinette dans la région de la Gatineau au Québec. For. Chron. 58:213-219.

Benoit, P.; Laflamme, G.; Bonneau, G.; Picher, R. 1983. Insectes et maladies des arbres, Québec — 1982. For. Conserv. 49:2-23.

Bess, H.A. 1946. Staminate flowers and spruce budworm abundance. Can. Dep. Agric., Forest Insect Invest., Ottawa. Bi-Mon. Prog. Rep. 2(2).

Blais, J.R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana* (Clem.), to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). Can. J. Zool. 30:1-29.

Blais, J.R. 1954. The recurrence of spruce budworm infestations in the past century in the Lac Seul area of northwestern Ontario. Ecology 35:62-71.

Blais, J.R. 1959a. Spruce budworm outbreaks and the climax of the boreal forest in eastern North America. Rep. Quebec Soc. Prot. P1.41:69-75.

Blais, J.R. 1959b. Incidence of overwintering parasites in post-outbreak populations of spruce budworm in Gaspé. Can. Dep. Agric., Div. For., Ottawa. Biol. Bi-Mon. Prog. Rep. 15(6).

Blais, J.R. 1960. Spruce budworm parasite investigations in the Lower St. Lawrence and Gaspé regions of Quebec. Can. Entomol. 92:384-396.

Blais, J.R. 1961. Spruce budworm outbreaks in the Lower St. Lawrence and Gaspé regions. For. Chron. 37:192-202.

Blais, J.R. 1964a. Account of a recent spruce budworm outbreak in the Laurentide Park region of Quebec and measures for reducing damage in future outbreaks. For. Chron. 40:313-323.

Blais, J.R. 1964b. History of spruce budworm outbreaks in the past two centuries in southeastern Quebec and northern Maine. Can. Dept. For., Entomol. Path. Br., Ottawa. Bi-Mon. Prog. Rep. 20(5).

Blais, J.R. 1965a. Parasite studies in two residual spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks in Quebec. Can. Entomol. 97:129-136.

Blais, J.R. 1965b. Spruce budworm outbreaks in the past three centuries in the Laurentide Park, Quebec. For. Sci. 11:130-138.

Blais, J.R. 1968. Regional variation in the susceptibility of eastern North American forests to budworm attack based on history of outbreaks. For Chron. 44:17-23.

Blais, J.R. 1980. Condition du sapin et de l'épinette blanche dans la région du parc des Laurentides en 1979 face à l'épidémie de la tordeuse et prévision des pertes. Serv. Can. For., Cent. Rech. For. Laurentides, Ste-Foy, Que. Rapp. Inf. LAU-X-43.

Blais, J.R. 1981a. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Can. J. For. Res. 11:620-629.

Blais, J.R. 1981b. Recurrence of spruce budworm outbreaks for the past two hundred years in western Quebec. For. Chron. 57:273-275.

Blais, J.R. 1983a. Les forêts de la Côte Nord au Québec sont-elles sujettes aux déprédations par la tordeuse? For. Chron. 59:17-20.

Blais, J.R. 1983b. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13:539-547.

Blais, J.R. 1983c. Predicting tree mortality induced by spruce budworm. For. Chron. 59:294-297.

Blais, J.R.; Archambault, L. 1982. Rating vulnerability of balsam fir to spruce budworm attack in Quebec. Can. For. Serv., Laurentian For. Res. Cent., Ste-Foy, Que. Inf. Rep. LAU-X-51.

Blais, J.R.; Martineau, R. 1960. A recent spruce budworm outbreak in the Lower St. Lawrence and Gaspé with reference to aerial spraying operations. For Chron. 36:209-224.

Bonneau, G.; Bordeleau, C. 1976. Evaluation quantitative et qualitative du parasitisme de la tordeuse des bourgeons de l'épinette. Pages 45-77 *in* Expertise entomologiques reliées aux pulvérisations aériennes contre la tordeuse des bourgeons de l'épinette au Québec en 1975 et prévisions pour 1976. Special Report Dep. Lands and For., Entomol. Pathol. Serv., Quebec, Que.

Brann, T.B.; Reams, G.A.; Solomon, D.S. 1983. Spruce budworm growth impact study 1981 report. Coop. For. Res. Unit, Maine Agric. Exp. Stn., Univ. Maine at Orono. CFRU Res. Note 11. 73 p.

Brown, C.E. 1970. A cartographic representation of spruce budworm (*Choristoneura fumiferana* (Clem.)) infestation in eastern Canada, 1909-1966. Can. For. Serv., Ottawa, Ont. Rep. 1263.

Clark, W.C.; Jones, D.D.; Holling, C.S. 1978. Patches, movements and populations dynamics in ecological systems: A terrestrial perspective. R.B.B. Institute of Animal Resource Ecology, University of British Columbia. Vancouver, B.C.

Dobesberger, E.J.; Lim, K.P.; Raske, A.G. 1983. Spruce budworm moth flight from New Brunswick to Newfoundland. Can. Entomol. 115:1641-1645.

Dowden, P.B.; Carolin, V.M.; Dirks, C.O. 1950. Natural control factors affecting the spruce budworm in the Adirondacks during 1946-48. J. Econ. Entomol. 43:774-783.

Elliott, K.R. 1960. A history of recent infestations of the spruce budworm in northwestern Ontario, and an estimate of resultant timber losses. For. Chron. 36:61-82.

Fye, R.E. 1963. The status of the spruce budworm in the Black Sturgeon Lake Region of Ontario. Can. Dep. For., For. Entomol. Path. Br., Ottawa. Bi-Mon. Prog. Rep. 19(2).

Gobeil, A.R. 1938. Dommages causés aux forêts de la Gaspésie par les insectes. Quebec Dept. Lands and For. Bull. 2:1-16.

Graham, S.A.; Orr, L.W. 1940. The spruce budworm in Minnesota. Univ. Minn. Agric. Exp. Stn. Tech. Bull. 142.

Greenbank, D.O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm. 1. The role of climate, Can. J. Zool. 34:453-476.

Greenbank, D.O. 1963a. The development of the outbreaks. Pages 19-23 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Greenbank, D.O. 1963b. Staminate flowers and the spruce budworm. Pages 174-180 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Greenbank, D.O.; Schafer, T.W.; Rainey, R.C. 1980. Spruce budworm moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. Mem. Entomol. Soc. Can. 110.

Hamel, L. 1978. Les conditions de déclenchement et de maintien d'une infestation de tordeuse des bourgeons de l'épinette. For. Conserv. 45:33-35.

Halliday, W.E.D. 1937. A forest classification for Canada. Can. Dept. North. Aff. Nat. Res., For. Br., For. Serv., Ottawa, Bull. 89.

Halliday, W.E.D.; Brown, A.W.A. 1943. The distribution pattern of some important trees in Canada. Ecology 24:353-373.

Hardy, Y.J. 1979. Les recherches sur la tordeuse des bourgeons de l'épinette. Revue forestière française. 31:217-223.

Hardy, Y.; Lafond, A.; Hamel, A. 1983. Epidemiology of the current spruce budworm outbreak in Quebec. For. Sci. 29:715-725.

Howse, G.W.; Harnden, A.A.; Meating, J.H.; Carrow, J.R. 1982. The 1980 spruce budworm situation in Ontario. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. Inf. Rep. O-X-336.

Ives, W.G.H. 1974. Weather and outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), Can. For. Serv., Northern For. Res. Cent., Edmonton, Alta. Inf. Rep. NOR-X 118.

Jaynes, H.A.; Drooz, A.T. 1952. The importance of parasites in the spruce budworm infestations in New York and Maine, J. Econ. Entomol. 45:1057-61.

Kettela, E.G. 1982. Spruce budworm infestations in Nova Scotia in 1982 and a forecast for 1983. Can. For. Serv., Maritimes For. Res. Centre., Fredericton, N.B. Tech. Note 63.

Kettela, E.G. 1983. A cartographic history of spruce budworm defoliation 1967-1981 in eastern North America. Can. For. Serv., Ottawa, Ont. Inf. Rep. DPC-X-14.

Kucera, D.R.; Taylor, R.G. 1983. Spruce budworm situation in North America 1982. U.S. Dep. Agric., Forest Service, Washington, D.C., Misc. Publ. 1436. 23 p.

Luciuk, G.S. 1984. Effect of climatic factors on post-diapause emergence and survival of spruce budworm larvae (Lepidoptera: Tortricidae). Can. Entomol. 116:1077-1083.

Martineau, R.;Lavallée, A.; Béique, R.; Davidson, J.G. 1976. Insectes et maladies des arbres, Québec — 1975. For. Conserv. 42:3-23.

MacLean, D.A. 1980. Vulnerability of fir–spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56:213-221.

MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. For. Chron. 60:273-279.

McGugan, B.M.; Blais, J.R. 1959. Spruce budworm parasite studies in northwestern Ontario. Can. Entomol. 91:758-783.

McLeod, J.M.; Blais, J.R. 1961. Defoliating insects on field spruce in Quebec. Can. Dept. For., For. Biol. Div., Ottawa, Ont. Bi-Mon. Prog. Rep. 17(1).

McLeod, J.M. 1977. Distribution of ovipositional attacks by parasitoids on overwintering larvae of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 109:789-796.

Miller, C.A. 1958. The measurement of spruce budworm populations and mortality during the first and second larval instars. Can. J. Zool. 36:409-422.

Miller, C.A. 1963. Parasites and the spruce budworm. Pages 228-244 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Miller, C.A.; Renault, T.R. 1976. Incidence of parasitoids attacking spruce budworm populations in New Brunswick. Can. Entomol. 108:1045-1052.

Mog, T.P.; Lynch, A.M.; Witter, J.A. 1982. Impact of the spruce budworm (Lepidoptera: Tortricidae) in Michigan Upper Peninsula. Great Lakes Entomol. 15:1-24.

Morris, R.F.; Miller, C.A.; Greenbank, D.O.; Mott, D.G. 1958. The population dynamics of the spruce budworm in eastern Canada. Proc. 10th int. Congr. Entomol. Vol. 4, 1956 (1958):137-149.

Morris, R.F., editor. 1963. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Neilson, W.W. 1963. Disease and the spruce budworm. Pages 272-287 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Pilon, J.G.; Blais, J.R. 1961. Weather and outbreaks of the spruce budworm in the province of Quebec from 1939 to 1956. Can. Entomol. 93:118-123.

Quebec Department of Lands and Forests. 1975. Suggestion d'un programme de recherche et de développement forestier en regard de la tordeuse. Special Report. Que. Dep. Lands For. Quebec, Que.

Quebec Government Office of Public Hearings on the Environment. 1983. Rapport d'enquête et d'audience publique sur le programme de pulvérisation aériennes contre la tordeuse des bourgeons de l'épinette. Annexe 2. Epidémiologie de l'insecte et efficacité de certaines solutions. 37p.

Rowe, J.S. 1972. Forest regions of Canada. Can. For. Serv., Ottawa, Ont. Publ. 1300.

Royama, T. 1984. Population dynamics of spruce budworm, *Choristoneura fumiferana* (Clem.): a reinterpretation of life table studies from the Green River Project. Ecol. Monogr. 54:429-462.

Sippell, W.L.; Rose, A.H.; Gross, H.L. 1970. *In* Annual report of the forest insect and disease survey. 1969. Can. Dep. Fish. For., Can. For. Serv., Ottawa, Ont.

Swaine, J.M.; Craighead, F.C. 1924. Studies on the spruce budworm (*Cacoecia fumiferana* (Clem.)) Part 1. A general account of the outbreak, injury and associated insects. Can. Dep. Agric., Ottawa, Ont. Tech. Bull. (New Ser.), 37:3-27.

Tothill, J.D. 1919. The passing of the balsam budworm in New Brunswick. Can. For. J. July:306-307.

Turner, K.B. 1952. The relation of mortality of balsam fir caused by the spruce budworm to forest composition in the Algoma forest of Ontario. Can. Dep. Agric., Ottawa, Ont. Publ. 875. 107p.

Webb, F.E.; Blais, J.R.; Nash, R.W. 1961. A cartographic history of spruce budworm outbreaks and aerial forest spraying in the Atlantic region of North America, 1949-1959. Can. Entomol. 93:360-379.

Webb, F.E.; Irving, H.J. 1983. My fir lady. For. Chron. 59:118-122.

Wellington, W.G.; Fettes, J.J.; Turner, K.B.; Belyea, R.M. 1950. Physical and biological indicators of the development of outbreaks of the spruce budworm and the forest tent caterpillar. Can. J. Zool. 30:114-127.

Yang, R.C.; Fry, R.D. 1981. Natural succession following harvesting in the boreal mixedwood forest. Pages 65-77 *in* Boreal Mixedwood Symp. Can. For Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. COJFRC Symp. Proc. O-P-9.

A Theory on the Effects of Diverse Host-Climatic Environments in British Columbia on the Dynamics of Western Spruce Budworm

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The genus *Choristoneura* is diverse and adaptable. Speciation is occurring rapidly in western North America in response to diverse habitats and hosts. Outbreaks of *C. occidentalis* occur in many plant communities over a range of precipitation levels but the last outbreak in British Columbia was restricted to an elevational belt within the Cascade Mountains. It is suggested that only in those stands where developmental temperatures permit overwintering larval emergence to be synchronized with bud swelling can larvae survive in large numbers. Early emergents cannot establish in new buds, and late emergents, when in the last instars, are exposed to an extended period of high mortality after budflush. Also, after budflush, food quality may decrease considerably. Through moth dispersal, western budworm maintains a broad heterogenetic base and a long emergence period to accommodate synchronization with the buds in stands which fall within favorable climatic elevational belts of the mountains. On an occasional year, at all elevations, limits are exceeded and asynchronization results in high mortality. Larval dispersal enables the budworm to search out buds in the stand which are best synchronized and have the highest food quality to maximize survival. If crop trees can be selected which exceed the limits of synchronization or food acceptability, it may be possible to improve the long-term outlook for reduced damage.

Le genre *Choristoneura* est diversifié et adaptable. En Amérique du Nord, les espèces se différencient rapidement, en réaction à la diversité des habitats et des hôtes. Les infestations de *C. occidentalis* touchent de nombreuses communautés végétales réparties selon la gamme de pluviosités, mais la dernière infestation en Colombie-Britannique s'est cantonnée à une hauteur précise dans la chaîne des Cascades. Il semblerait que ce n'est que dans les peuplements où les températures de développement permettent la synchronisation de l'émergence des larves qui ont hiverné et du bourgeonnement, que les larves survivent en grand nombre. Si celles-ci sortent trop tôt, elles ne peuvent se fixer dans les nouveaux bourgeons, tandis que si elles sortent tard, elles sont exposées, aux derniers stades larvaires, à une période prolongée de forte mortalité après le débourrement. En outre, après le débourrement, la qualité de la nourriture peut considérablement diminuer. Grâce à la dispersion des imagos, la tordeuse occidentale s'assure une base hétérogène large et une longue période d'émergence qui permet de la synchroniser avec le bourgeonnement dans les peuplements montagnards aux altitudes et au climat favorables. En certaines années, à toutes les altitudes, les limites sont dépassées et le décalage chronologique provoque de fortes mortalités. La dispersion des larves permet à la tordeuse de rechercher, dans le peuplement, les bourgeons dont l'évolution est le plus synchronisée à ses besoins et qui constituent la nourriture de la plus haute qualité, afin de maximiser sa survie. Si on pouvait sélectionner des arbres de peuplement final qui excèdent les limites de la synchronisation ou de l'acceptabilité trophique, on pourrait réduire les dommages à long terme.

Diversification of *Choristoneura*

The "conifer-feeding budworms" in western North America are a large complex of partially isolated, partially interbreeding, and partially speciated populations living in *Pseudotsuga*, *Abies*, *Picea* and *Pinus* forests from Alaska to southern California (Powell 1980). This state of speciation and distribution probably reflects the influence of glaciation and the reoccupation of the deglaciated land by forests and their associated insects. Almost all of British Columbia was denuded by ice and the land surface was remoulded (Matthews 1979). Wet and temperate Pacific air masses moved across high mountain ranges alternately dropping large volumes of precipitation on the windward slopes and absorbing moisture from the lee sides. Temperatures ranged from deep arctic lows in winter to desert-like highs in the summer (Danks 1979). This diverse geography and climate could only be reoccupied by organisms with a high degree of diversification. The budworm has succeeded because it is flexible and adaptable, feeds on many hosts, flourishes in various climates, and has an aggressive capability to spread and occupy new forests.

The adaptability of the genus *Choristoneura* is evident in the complex of closely related species and their diverse geographical distributions (Harvey 1985). *Choristoneura occidentalis* Freeman occupies the central position, on its host Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) which, after deglaciation, probably spread northward from Washington through the warmer sites of southern British Columbia. A closely related species, *C. biennis* Freeman, was able to adopt a two-year life cycle, through selection for a second diapause, and occupy the cooler subalpine fir and Engelmann spruce forests (*Abies lasiocarpa* (Hook) Nutt. and *Picea engelmanii* Parry) of the high mountains (Shepherd 1961). *Choristoneura orae* Freeman may be a remnant of preglacial times which survived the glacial period in the Alaskan–Yukon refugia (Scudder 1979), because it is adapted to the cool Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) rain forests of the north coast. *C. fumiferana* is a resident of the *Picea* – *Abies* boreal forest which extends across Canada and into northern British Columbia, Yukon, and Alaska. The distribution of all these budworm species may meet and sometimes overlap in central British Columbia. The lack of distinctive morphological characteristics among these species makes identification difficult in this region.

In Oregon and California there are also overlapping populations of *C. occidentalis, C. carnana* (Barnes and Busck), and *C. retiniana* (Walsingham), which are hard to distinguish (Volney 1985). It is interesting that *C. retiniana*, which occurs south of the glacial limits, has a similar pheromone to *C. orae* of Alaska and northwest British Columbia (Daterman et al. 1984; Gray et al. 1984). Pine forests in California and Oregon ofter occur in mountainous areas separated by wide dry valleys, which provide a degree of isolation. Three or four subspecies of *C. lambertiana* (Busck) are found in these areas and are hard to distinguish (Powell 1980). Western North America seems to be the center of speciation of the genus where the wide range of available habitats has offered *Choristoneura* the opportunity to diversify onto many hosts growing in a variety of climates. The species which causes most damage in western North America is *C. occidentalis*.

The remainder of this paper deals with the geographical relationships of *C. occidentalis* in British Columbia, the importance of synchronization of larval emergence with host bud swelling, the strategies the tree uses in responding to the budworm, and the strategies the budworm uses to survive and succeed in a variable environment. No attempt is made to review other theories on the dynamics of the budworm, but only how synchrony, foliage quality, and dispersal may affect budworm population ecology. For more complete coverage of other theories see Blais (1985), McKnight (1971), Royama (1984), and Wellington et al. (1950). Throughout this discussion, outbreaks are defined as populations of budworm numerous enough to cause defoliation that can be noticed and mapped from the air.

Geographical Relationships

The geographical pattern of budworm outbreaks in British Columbia varies from that of other defoliators. Many defoliators in British Columbia rise to outbreak levels for only short periods in any one stand. Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)), forest tent caterpillar (*Malacasoma disstria* Hubner), western hemlock looper (*Lambdina fiscellaria lugubrosa* (Hulst)), and many other geometrids quickly increase, defoliate trees for one to four years, and then drop to low levels again (Shepherd 1977). Western spruce budwom is the exception. Population fluctuations are irregular and unpredictable. Outbreaks can collapse after one or two years or can last for several years in a particular stand (Harris et al. 1985; Johnson and Denton 1975). Numbers of budworm often increase to outbreak levels, decrease, and recover to outbreak levels again. Populations in any one valley are often synchronous. Within that valley trends upward or downward are similar, regardless of the population density of budworm in a particular stand. Meanwhile, populations within another valley, 300 km (186 mi.) away, may again be synchronized, but the trends can be different between the two valleys. The only factor I know that can regulate populations either directly or indirectly at that geographic scale is climate.

Some insect species require specific environmental conditions before they can reach outbreak levels which occur only in certain sites (Andrewartha and Birch 1954; Shepherd 1977). Those conditions may also be reflected in the plant communities present. Therefore, there is often a close association between the distribution of specific plant communities and the distribution of outbreaks of some insect species. This association appears to be more pronounced in the more extreme conditions of the host's range. The black-headed budworm (*Acleris gloverana* Walsingham), for instance, has outbreaks in the wettest hemlock community of Vancouver Island (Shepherd 1977). The outbreaks do not extend into the adjacent dry hemlock or Douglas-fir communities. In contrast, outbreaks of Douglas-fir tussock moth are restricted to the hottest and driest communities within the range of Doulgas-fir, and outbreaks of two-year cycle spruce budworm in the Canadian Rockies occur only in a specific plant community of the high altitude, cool, alpine fir/Engelmann spruce forests (Shepherd 1959). Again, the western spruce budworm is an exception. Outbreaks are not restricted to one or two communities, but occur from the moist forests of the mixed coastal-interior forests to the dry interior forests, covering a range of communities which vary considerably in amount of precipitation received (Shepherd 1977).

Outbreaks are restricted, however, by elevation. They appear as a belt in the mid-slope areas of the mountains, with populations decreasing above and below those elevations. Wulf and Cates (in press) also report that defoliation in Idaho and Montana is more common at mid to upper elevations and covers a range of habitat types. Preliminary investigations in British Columbia indicated that host distribution was not related to this elevation effect nor was moth dispersal, as moths readily moved into and laid eggs in stands above and below the defoliated belt. The effect had to be realized through differential survival. The actual elevation of maximum defoliation varies from year to year and place to place so that the location of the zone most favorable for budworm varies considerably and is not associated with a particular plant community or stand condition. Elevation belts of other insect or disease conditions in mountainous situations have been related to specific temperatures (Stark 1958, 1959; Shepherd 1977; MacHattie 1963; Henson 1952; Baltensweiler 1984) and I suggest that the distribution of outbreaks of the western spruce budworm is also related to temperature.

Large-scale patterns of outbreaks in British Columbia indicate the center of budworm defoliation has moved gradually to the northeast over succeeding years, following the prevailing wind flow pattern (Figure 1). In July, during the flight period, there is strong daytime heating of the air in the principal valleys of the Fraser and Thompson rivers resulting in uplifing and strong replacement winds flowing inland from the cool Pacific Ocean. The large mountains of the Cascade Range force the winds to funnel up the valleys with the strongest winds occurring in late afternoon and continuing well after sunset. As the sun sets, radiation cooling begins on the shaded slopes and a thin layer of cool air begins sliding downslope. The time of turnaround in wind direction varies with the direction of slope exposure. Winds on the east and north-facing slopes reverse their direction earlier than on west or south-facing slopes. The daytime pattern of wind flow persists longer after dark in the main valleys than in the smaller side valleys. These winds are quite consistent under clear skies but if cloudiness blocks heating or pressure gradients reverse, the winds will slow or change direction so that year to year changes in frequency do occur, but in most years the prevailing direction is toward the northeast (personal communication, R. Silversides, Canadian Forestry Service, Victoria, British Columbia).

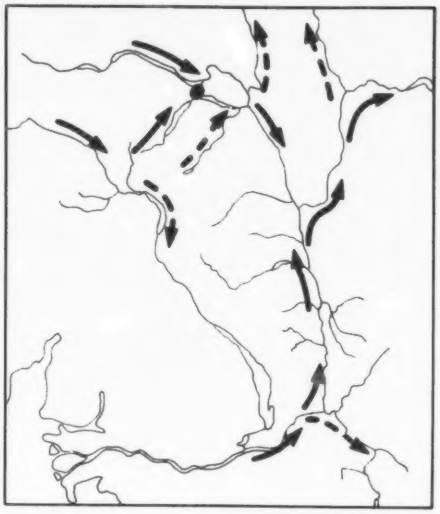

Figure 1. Direction of prevailing diurnal winds in S.W. British Columbia during the moth flight period. Mission Pass designated by a spot.

Male and female (*C. occidentalis*) moths begin flying at dusk and carry on for 2 or 3 hours after sunset, depending on temperature (Shepherd 1979). This occurs during the period of wind turn-around and direction of moth drift varies with each situation. In most years, though, dispersing females are transported in the same direction, seeding-in downwind stands. The effect of the immigrants on the indigenous insect densities is probably most marked in the preoutbreak low-density period when a relatively low number of immigrant moths can double or triple the population density. This sustained accumulation over a number of years probably hastens the outbreak.

There is an interesting example of a zone of wind convergence in British Columbia where two large budworm-spawning valleys come together at Mission

Pass above Seton Lake near Lillooet (Figure 1). There have been four outbreaks in British Columbia east of the Cascade Mountains since 1909. These upper slopes above Seton Lake have been defoliated in every outbreak and are often the first to become so (Harris et al. 1985).

Moth dispersal is an adaptation which allows the insect to spread its risks over many stands and survive wherever favorable situations occur. The environment varies in both time and space and the distribution of outbreaks coincides with the distribution of sites where conditions favorable for increase occur most often. In British Columbia, the location of these conditions is at mid-slope, resulting in elevation belts of defoliation.

Strong dispersal has another advantage for which I have coined the term "nomadic" strategy of survival. This strategy is more obvious with an insect like forest tent caterpillar where mortality factors like disease, parasitism, starvation through overpopulation and, perhaps, induced host resistance rapidly overtake the population (Hodson 1941). Only by dispersing to new stands at every generation can the population escape heavy depredation. This nomadic strategy may also play a role, at least in part, with budworm.

Synchronization with the Host

The time of larval emergence and dispersal relative to bud development is critical. Larvae go through two dispersal periods before feeding — one in August just after egg-hatch and another in spring just after emergence from overwintering. Behavior of *C. occidentalis* is similar to *C. fumiferana* at this stage. *C. fumiferana* larvae stream off the trees on silk threads carried by the wind until the silk touches and sticks to an object (Batzer 1968). Unless there are strong vertical air currents, the surrounding trees are the usual recipients and screen out the larvae. Larval dispersal redistributes larvae over the surfaces of the crowns which results in reduced competition and maximum occupation of all buds that are in a suitable stage of development.

The larvae prefer to penetrate swollen buds and live in an ideal natural greenhouse where it is warm, well protected, and where there is an abundance of freshly-growing food (Wellington 1948). If the larvae hatch too early, they cannot penetrate the tough bud scales and are forced to feed on mature needles (McGugan 1954). In Douglas-fir, the production of flower buds is quite sporadic and is unlikely to influence long-term population trends. There also appears to be a territorial behavior in *C. occidentalis,* restricting occupancy to one budworm per bud (McDonald 1979). Redistribution continues until the larvae are quite large (Beckwith and Burnell 1982). Populations are thus reduced to the carrying capacity of the host and losses due to competition would be expected to be directly related to population density above the bud complement of the trees (Thomson 1979). The effect may be a great loss of young larvae but the process tends to ensure maximum population survival.

Weekly observations of bud and insect development in 100 marked buds at each of many sites located at different elevations in southern British Columbia indicated that population trends during the larval period can be divided into three phases, depending upon the development of the host buds (Figure 2): 1) a needle-mining phase which occurs before larvae can penetrate the hard overwintering buds, 2) a protected phase where larvae live inside developing buds, and 3) an exposed phase after buds flush and larvae have lost their protection. Techniques to establish these developmental phases are given in Shepherd (1983). During needle mining, larvae emerge from overwintering diapause, are unable to penetrate the tight buds, and are forced to mine old needles which suffer rapid abscission (McGugan 1954); many larvae are lost as they search for suitable buds (Figure 2). In contrast, larvae that emerge after buds have swollen mine directly into the buds and few larvae are lost. During this protected phase, large increases in larval density may occur as larvae continue to emerge from diapause and mine buds. Maximum larval density in buds usually occurs just before flush, although, in cases of poor synchronization, the maximum number can occur during needle mining. As soon as the buds flush, the larvae lose their protection and survival drops rapidly. Birds and ants are primary predators of *C. occidentalis* larvae and pupae in the open shoots (Campbell and Torgersen 1983). Predators are often compensatory, i.e., as bird predation decreases, ant predation increases, and *vice versa*. However, from the budworm point of view the type of predator is immaterial; more important is the length of time of exposure to predation. The daily loss rate is almost constant during this period (Campbell and Srivastava 1984) and percent survival plotted over days of exposure results in an exponential curve (Figure 3).

Contrasting synchronization between bud development and larval emergence occurred in my study sites between 1979 and 1980 (Figure 2). In 1979, bud development was advanced enough for emerging larvae to penetrate the buds directly and survival was good in the younger instars. However, the buds flushed early and the exposed period before pupation was lengthy. Survival declined and was close to zero by the pupal stage. In 1980, larvae emerged before the buds were swollen, and loss was high while the larvae mined old needles. Larvae which emerged late successfully occupied the newly swollen buds. Bud flush was late relative to insect development resulting in a short exposure period and good survival of late instars. The resultant survival of the 1980 population was much greater than that of the 1979 population.

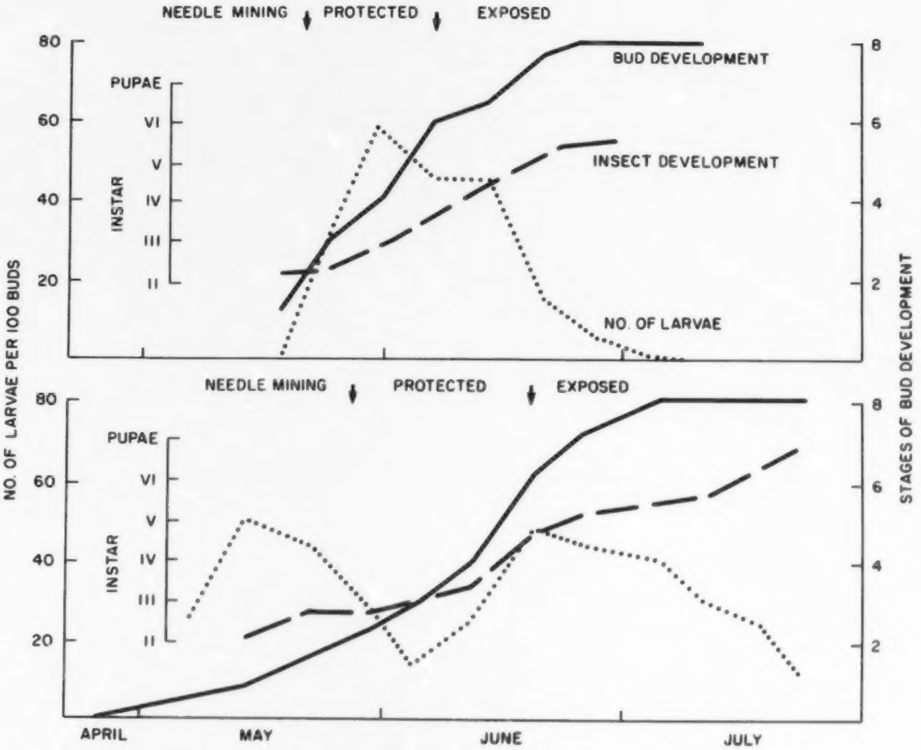

Figure 2. Comparison in population trends between two years with different synchronization of bud and budworm developments. The three phases in population trends during the larval period are indicated.

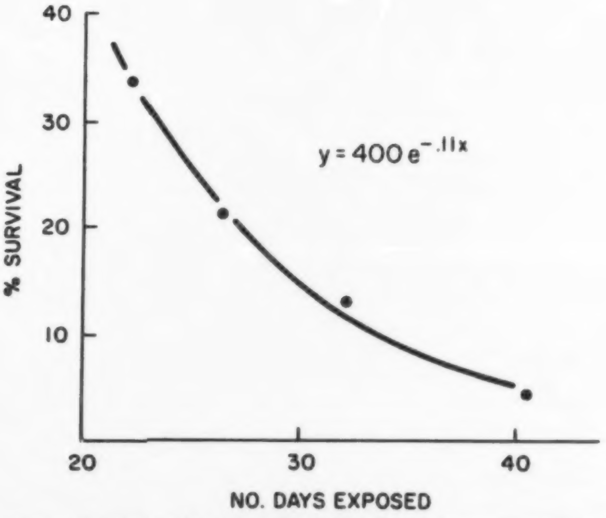

Figure 3. Relationship between the length of the exposure period between budflush and pupation and percent survival between maximum budworm density and pupation.

Maximum survival would be expected to result from good synchronization between bud swelling and larval emergence; a long period between bud swelling and budflush and a short period between budflush and moth emergence. The weather that would result in this development pattern would be, presumably, an average spring with no prolonged warm spells in March or April, ensuring good synchronization between bud swelling and larval emergence. After larvae enter the buds, cool temperatures which slow down bud development would be the most favorable, but, after budflush, hot dry weather would speed larval development and decrease exposure time. Beckwith and Kemp (1984) have compared shoot growth of grand fir and Douglas-fir for different crown levels as related to degree-days. Their models adequately predict shoot growth from temperature, indicating that bud developmental stages can be predicted, given adequate temperature records. The study by Thomson et al. (1983) on the effects of elevation on budworm development also provides a useful predictive model.

The synchronization between budflush and larval emergence depends upon developmental temperatures which vary considerably with elevation and between years (Hermann, in press). In an experiment where overwintering larvae were set out at different elevations, larvae at the valley bottom emerged long before buds were ready to be mined, and were lost, whereas at higher elevations, emergence and bud swelling coincided (R.F. Shepherd, unpublished data). Occasionally years occur when spring temperatures are unfavorable for good synchronization at all elevations and populations drop drastically. In contrast, there are also years when populations greatly increase. Ives (1974), Thomson et al. (1984), and Wellington et al. (1950) have all related weather patterns or extremes in temperatures to occurrences or collapses of eastern or western budworm outbreaks.

In New Brunswick, emergence of *C. fumiferana* usually occurs before bud swelling on black spruce (*Picea mariana* (Mill.) B.S.P.), and this tree species is being planted to minimize budworm damage, although the degree of asynchrony may vary year by year depending on weather. In Newfoundland, with different spring temperatures and a different provenance of black spruce (but with the same genetic stock of budworm as in New Brunswick [Dobesberger et al. 1983]), the high level of black spruce damage may be related to a much closer synchronization between bud swelling and larval emergence.

There is also great variability in defoliation by *C. occidentalis* among trees within stands (McDonald 1981). Many trees which are exposed to the same attack, density, and weather conditions support different population densities. This may be related to phenology. Insect survival would probably be lower on early- or late-flushing trees.

Blais (1957), Eidt and Cameron (1971), Eidt and MacGillivray (1972), and Wulf and Cates (in press) recognized the importance of synchronization of budflush with larval emergence of *C. fumiferana*. They showed how differences in dates of flushing between different host species and between individual balsam fir trees, manipulated experimentally by cold treatment, influenced rates of larval establishment. Greenbank (1956) also recognized that synchronization could be important and suggested that during increasing trends leading to an outbreak, larval development was probably more advanced relative to bud development, thus decreasing the time of exposure.

It appears that *Choristoneura* populations are able to maintain flexibility by having a wide emergence period which allows cohorts to be available whenever buds are susceptible to mining. However, after those cohorts are established, their course is fixed and they are vulnerable to reactions and vacillations of the host and to the weather.

Tree Strategies

It is necessary to understand the interaction between the host tree and the budworm and the response of the tree to attack if we wish to reduce budworm impact through enlightened forest management. Trees are a dynamic part of the interaction and their variability and response must be considered.

Some slow-growing, and long-lived trees contain relatively high amounts of chemicals, such as tannins which are deterrents to insect feeding. Production of these chemicals may provide adequate protection but at a high metabolic cost (Feeny 1975). An alternative for plants is to be short lived, fast growing, highly reproductive and widely dispersive so they can avoid attack. A third possible strategy would be for the tree to be fast growing but, if attacked, to quickly respond by producing allelochemicals. The latter is the most efficient strategy but it does encounter high risks, especially with conifers where only the actively growing tissues, such as new foliage, are capable of responding.

A close correlation in timing between the flush of oaks and the early feeding stages of winter moth (*Operophtera brumata* (L.)), and oak leaf roller (*Tortrix viridana* L.), has already been noted by Feeny (1975) and Schütte (1960). The tannin content of oak leaves increased from a low level in April to 2.4 percent in September while the presence of as little as 1 percent caused a significant reduction in larval growth and pupal weight of winter moth. Thus, insects that hatched before flush starved to death and those that hatched well after flush suffered because they were forced to feed on older foliage with higher tannin contents. As a result, trees within an oak forest which were not synchronized with egg hatch suffered less damage than those closely synchronized.

It is also possible that damage in one year may induce changes in allelochemicals in the new foliage in subsequent years (Schultz and Baldwin 1982). Haukioja and Niemela (1977) found pupation was delayed when geometrid larvae (*Oporinia autumnata* Bkh.) were fed leaves collected from birch trees from which adjacent leaves had been mechanically torn two days earlier. Also there was still a detectable delay when larvae were fed with new undamaged leaves taken from a plant which suffered leaf damage two years previously. A foliage reaction such as this would be expected to vary considerably between trees and could result in large differences in subsequent infestation rates.

Trees vary considerably in the quality and quantity of terpenes produced and this may be one of the reasons for the differences in population densities noticed among trees in any stand (Hermann, in press; Wulf and Cates, in press). In addition to the production of secondary chemicals, reactions by the host could include a reduction in needle size, nutritional levels, or physical food quality, as occurs with reaction to feeding by the larch bud moth (*Zeiraphera diniana* Gn.), (Baltensweiler 1984), or an increase in secondary bud production to overcome the effects of defoliation. The latter is obvious with some *Pseudotsuga* attacked by budworm. As Doskotch et al. (1981) pointed out, much work on nutritional content of foliage has shown that it does not vary much among species or individuals and it is generally adequate. Attention has now shifted to the secondary chemicals which are produced in the foliage. These vary considerably among species and individuals and often act as deterrents to attack by insects. Production of these secondary chemicals may change in response to insect damage or host stress situations.

The concentration of feeding deterrents in foliage varies considerably during the time of shoot development and the feeding period of the larvae. As an example of the type of interaction that may be involved, note the fluctuations in quality and quantity of terpenes in foliage (von Rudloff 1972, 1975; Hunt and von Rudloff 1974). Von Rudloff and Granat (1982), von Rudloff and Rehfeldt (1980), and von Rudloff (1972) have shown, for a number of conifers including *Picea* and *Abies*, that the relative terpene contents are quite stable in foliage older than 6 months, but there are considerable fluctuations within the buds and shoots just before and after flush. For example, in the first week of May, before white spruce flushes, the buds contain mainly α-pinene, liminene, myrcene, and β-pinene. By the end of May, the percentage of α- and β-pinene in young leaves has decreased to a minimum. Thereafter, the percentages change again and by mid-June have reached the high levels typical of fall and mid-winter foliage. Entirely different sequences in the change were recorded for other major terpenes. Bornyl acetate rose from trace amounts in the buds to an early maximum in the shoots late in May and thereafter the relative amounts dropped gradually to low relative percentages which are typical of fall and winter foliage. Two weeks after the rise in bornyl acetate, the relative percentage of camphor rose dramatically to about 35 percent of the total terpene content and remained at that level thereafter. Thus, small changes in the time of feeding could make large differences in the types of terpenes with which the larvae have to contend. Cates et al. (1983a), using synthetic diets, showed that bornyl acetate had adverse effects upon *C. occidentalis* larvae but β-pinene had favorable effects.

Cates et al. (1983a, 1983b) also investigated foliage chemistry and found significant correlations between the terpene content of Douglas-fir trees and larval density and dry weight of adult female western spruce budworm. They did not sample at different times and so could not measure the effects of synchronization between these factors, but they found the time of budburst to be significant in a multiple regression, so an interaction was probably present. They also found that trees on a moisture-stressed site had less suspected feeding-resistant terpenes in their foliage than needles of nonstressed trees growing on a north-facing slope.

Mattson et al. (1983) found significant negative correlations between terpene levels in foliage and weight gain of *C. fumiferana* larvae, and Heron (1965) found that pungenin, which has a deterrent effect on feeding by *C. fumiferana* larvae, occurs at low levels in new shoots and at high levels in mature needles. A review of the role of terpenes in tree resistance has been given by Hanover (1975) and Stark (1965). Similarly, Durzan (1968), Durzan and Lopushanski (1968), and Durzan and Steward (1963), have shown that there are large changes in seasonal and diurnal amounts of amino acids and related compounds in foliage. Greenbank (1956) found *C. fumiferana* that were delayed in their emergence and fed on older current foliage, were smaller and less fecund. More recently, Kay (1983) found that current foliage of a resistant Douglas-fir, when cut and fed to a geometrid defoliator, resulted in the death of the insects. Larvae fed 1-year-old or 2-year-old foliage from the same tree or all years of foliage from adjacent nonresistant trees survived well and grew to normal pupal weights. This indicates a biologically active chemical is probably being synthesized in actively growing tissue.

Budworm Strategies

I have mentioned that dispersal aids the insect in coping with wide variations in weather, date of budflush, and food quality. Similarly, larval dispersal helps the insect contend with the wide range in phenology and terpene levels exhibited by individual trees by spreading the risks of survival over many trees. In a variable environment, each year there is a strong selection pressure in favor of larvae which emerge during a specific time period when the buds are receptive. There is a continuous shifting of genetic selection for early or late emergence. What is favorable one year will be unfavorable another year. Budworm populations would be rapidly reduced were it not for their strong dispersal characteristics. The mixing of the population maintains a high degree of heterogeneity and a wide range in the time of larval emergence (Volney et al. 1983), enabling the insect to cope with environmental conditions.

We have noted that moths and larvae which spread over the area help ensure that, under severe conditions, at least some will find an acceptable habitat and survive. The strategy is to overproduce and accept high losses to ensure that some will succeed. However, in years when conditions are favorable over most of the stands, there can be an explosion in numbers because populations are being generated over a much larger area in conjunction with an increase in survival rates for any particular location.

Forest Management Strategies

Forest management requires the prediction, in time and space, of budworm trends. This is not easy, because under the driving influence of weather, timing of events could be just as important as the magnitude of the event. Different elements of prevailing weather are important at different times and indirect effects of weather are largely unknown. For instance, high temperatures through September and October could be deleterious to overwintering larvae (Ives 1974; Thomson et al. 1984) but high temperatures between budflush and moth emergence could be advantageous to feeding larvae by reducing the length of the exposed period. Perhaps weather, as a regulating factor, only comes into play during years of extremes, causing dramatic population changes (Thomson et al. 1984). Other factors may have more impact in average years, making trend analysis difficult. A pheromone moth trapping system capable of measuring low budworm levels may help indicate where and when outbreaks might occur.

Silvicultural programs to minimize the effects of budworm are being formulated. Generally, the forester would like to reduce the amount of budworm-susceptible foliage and increase the amount of nonsusceptible foliage. He can do this in two ways: convert to a nonhost species or convert to resistant strains of trees selected from among normal host species. Conversion to a nonhost species is a good strategy, provided the site is suitable for that species and growth rates and economics are acceptable. For instance, proposals have been made to reduce the amount of susceptible climax species on the warm dry sites of the forests of northern Idaho and western Montana (Carlson et al., in press) by planting seral species, such as lodgepole or ponderosa pine, in place of the susceptible climax species. Provided these replacement species are managed on an appropriate rotation, there should be a minimum of other pest problems so that one is not just shifting problems rather than solving them. Often, though, there is little choice of alternative species on budworm-susceptible sites as the loss in growth rates or values is too great to be acceptable. In budworm-susceptible Douglas-fir forests of British Columbia, for example, no other acceptable species seem ecologically adapted to these sites. The only answer, in this case, for a long-term reduction of budworm, is to identify and propagate resistant strains.

Agriculture has been successfully using resistant strains for a long time (Painter 1966), and McDonald (1979, 1980, 1981) has carried out some interesting studies in this direction for budworm. At the same time, a study of historical defoliation patterns should reveal those sites where significant defoliation occurs most frequently. Planting resistant strains within those sites could reduce both damage and the downwind spread of populations. We are not attempting complete eradication by such a procedure. A reduction of impact of perhaps 50 to 80 percent may be quite attainable and acceptable.

The usual argument against this approach is that the insect can adapt to strains faster than we can produce them because of the large number of generations it passes through during only one generation of its host plant. But, as I previously suggested, the budworm is highly dependent on maintaining a heterogenetic population: it is a necessity to survive in a variable environment. There are sufficient forests which will not be cut because of inaccessibility, wilderness, park reserves, etc., to maintain the heterogeneity of the budworm and prevent the establishment of an insect population adapted to the resistant trees. Therefore, let us take advantage of this characteristic and turn it against the budworm by identifying, propagating, and planting resistant trees on the susceptible, productive sites.

Literature Cited

Andrewartha, H.G.; Birch, L.C. 1954. The distribution and abundance of animals. Univ. Chicago Press. Chicago, Ill.

Baltensweiler, W. 1984. The role of environment and reproduction in the population dynamics of the larch bud moth, *Zeiraphera dinianan* Gn. (Lepidoptera, Tortricidae). Pages 291-302 *in* W. Engels et al. eds. Advances in Invertebrate Reproduction 3. Elsevier Science Publishers, Amsterdam.

Batzer, H.O. 1968. Hibernation site and dispersal of spruce budworm larvae as related to damage of sapling balsam fir. J. Econ. Entomol. 61:216-220.

Beckwith, R.C.; Burnell, D.G. 1982. Spring larval dispersal of western spruce budworm in north-central Washington. Environ. Entomol. 11:828-832.

Beckwith, R.C.; Kemp, W.P. 1984. Shoot growth models for Douglas-fir and grand fir. For. Sci. 30(3):743-746.

Blais, J.R. 1957. Some relationships of spruce budworm, *Choristoneura fumiferana* (Clem.) to black spruce, *Picea mariana* (Moench) Voss. For. Chron. 33:364-372.

Blais, J.R. 1985. The ecology of the eastern spruce budworm: a review and discussion. Pages 49-59 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Campbell, R.W.; Srivastava, N. 1984. Day-to-day survival of late instar western spruce budworm larvae and pupae. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Note PNW-408. 5p.

Campbell, R.W.; Torgersen, T.R. 1983. Compensatory mortality in defoliator population dynamics. Environ. Entomol. 12:630-632.

Carlson, C.E.; Schmidt, W.C.; Fellin, D.G.; Wulf, N.W. (in press). Silvicultural approaches to western spruce budworm management in the Northern Rocky Mountains. *In* Chapter 7, M.H. Brookes, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech. coords. Managing trees and stands susceptible to western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1695.

Cates, R.G.; Redak, R.A.; Henderson, C.B. 1983a. Natural product defensive chemistry of Douglas-fir, western spruce budworm and forest management practices. Z. Angew. Entomol. 96:173-182.

Cates, R.G.; Redak, R.A.; Henderson, C.B. 1983b. Patterns in defence natural product chemistry: Douglas-fir and western spruce budworm interactions. Pages 1-19 *in* P. Hedin, ed. Plant resistance to insects. American Chemical Society Symposium, Series 208, Washington, D.C.

Danks, H.V. 1979. Physical basis for Canadian regional diversity. Pages 7-30 *in* Canada and its insect fauna. Mem. Entomol. Soc. Can. 108.

Daterman, G.E.; Cory, H.T.; Sower, L.L.; Daves, G.D., Jr. 1984. Sex pheromone of a conifer-feeding budworm, *Choristoneura retiniana*, Walsingham. J. Chem. Ecology 10:153-160.

Dobesberger, E.J.; Lim, K.P.; Raske, A.G. 1983. Spruce budworm (Lepidoptera: Tortricidae) moth flight from New Brunswick to Newfoundland. Can. Entomol. 115:1641-1645.

Doskotch, R.W.; O'Dell, T.M.; Girash, L. 1981. Phytochemicals and feeding behavior of gypsy moth larvae. Pages 657-666 *in* C.C. Doane and J.L. McManus. The gypsy moth: research toward integrated pest management. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1584.

Durzan, D.J. 1968. Nitrogen metabolism of *Picea glauca* (Moench) Voss-I. Seasonal changes of free amino acids in buds, shoot apices and leaves, and the metabolism of [U-C^{14}]-L- arginine by buds during the onset of dormancy. Can. J. Bot. 46:909-919.

Durzan, D.J.; Lopushanski, L. 1968. Free and bound amino acids of spruce budworm larvae feeding on balsam fir and red and white spruce. J. Insect Physiol. 14:1485-1497.

Durzan, D.J.; Stewart, F.C. 1963. The nitrogen metabolism and seasonal changes in shoots of *Picea glauca* (Moench) Voss. Plant Physiol. 38 Suppl. p.vi.

Eidt, D.C.; Cameron, M.D. 1971. Delayed budbreak and spruce budworm survival. Can. For. Serv., Ottawa, Ont. Bi-mon. Res. Notes 27:28-29.

Eidt, D.C.; MacGillivray, H.G. 1972. Resistance of seven fir species to spruce budworm and other insects. Can. For. Serv., Ottawa, Ont. Bi-mon. Res. Notes 28:2-3.

Feeny, P. 1975. Plant apparency and chemical defence. Recent advances in Phytochemistry 10:1-40.

Gray, T.G.; Slessor, K.N.; Grant, G.G.; Shepherd, R.F.; Holsten, E.H.; Tracey, A.G. 1984. Identification and field testing of pheromone components of *Choristoneura orae* (Lepidoptera: Tortricidae). Can. Entomol. 116:51-56.

Greenbank, D.O. 1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. Can. J. Zool. 34:453-476.

Hanover, J.W. 1975. Physiology of tree resistance to insects. Ann. Rev. Entomol. 20:75-95.

Harris, J.W.E.; Alfaro, R.I.; Dawson, A.F.; Brown, R.G. 1985. The western spruce budworm in British Columbia, 1909-1983. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Inf. Rep. BC-X-257.

Harvey, G.T. 1985. The taxonomy of the coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): A review. Pages 16-48 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Haukioja, E.; Niemela, P. 1977. Retarded growth of a geometrid larva after mechanical damage to leaves of its host tree. Ann. Zool. Fennici 14:48-52.

Henson, W.R. 1952. Chinook winds and red belt injury to lodgepole pine in the Rocky Mountain Parks area of Canada. For. Chron. 28:62-64.

Hermann, R.K. (in press). Description of host species. *In* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech. coords. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1694.

Heron, R.J. 1965. The role of chemotactic stimuli in the feeding behavior of spruce budworm larvae on white spruce. Can. J. Zool. 43:247-269.

Hodson, A.C. 1941. An ecological study of the forest tent caterpillar *Malacosoma disstria* Han. in northern Minnesota. Univ. Minnesota Agr. Sta. Tech. Bull. 148.

Hunt, R.S.; von Rudloff, E. 1974. Chemosystematic studies in the genus *Abies*. 1. Leaf and twig oil analysis of alpine and balsam firs. Can. J. Bot. 52:477-487.

Ives, W.G.H. 1974. Weather and outbreaks of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae) Can. For. Serv., North. For. Res. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-118.

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of the western spruce budworm in the American Northern Rocky Mountain area from 1922 through 1971. U.S. Dep. Agric., For. Serv., Intermountain For. Range Exp. Sta., Ogden, UT. Gen. Tech. Rep. INT-20.

Kay, M. 1983. Resistance of Douglas-fir to *Pseudocormia suavis*. New Zealand J. For. Sci. 13:46-52.

MacHattie, L.B. 1963. Winter injury of loagepole pine foliage. Weather 18:301-307.

Matthews, J.V. 1979. Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. Pages 31-86 *in* H.V. Danks. Canada and its insect fauna. Mem. Entomol. Soc. Canada. 108.

Mattson, W.J.; Slocum, S.S.; Killer, C.N. 1983. Spruce budworm (*Choristoneura fumiferana*) performance in relation to foliar chemistry of its host plants. Pages 55-56 *in* R.L. Talerico and M. Montgomery. Forest defoliator-host interactions: a comparison between gypsy moth and spruce budworm. U.S. Dep. Agric., For. Serv., Northeastern For Exp. Stn., Broomall, PA. Gen. Tech. Rep. NE-85.

McDonald, G.I. 1979. Resistance of Douglas-fir to western spruce budworm: Results of a preliminary progeny test. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn., Ogden, UT. Res. Note INT-264.

McDonald, G.I. 1980. Progeny testing of Douglas-fir seedlings for resistance to western spruce budworm. Pages 460-465 *in* Resistance to diseases and pests in forest trees. Workshop proceedings. Pudoc, Wageningen, The Netherlands.

McDonald, G.I. 1981. Differential defoliation of neighboring Douglas-fir trees by western spruce budworm. U.S. Dep. Agric., For. Serv., Intermountain For. and Range. Exp. Stn., Ogden, UT. Res. Note INT 306.

McGugan, B.M. 1954. Needle-mining habits and larval instars of the spruce budworm. Can. Entomol. 86:439-454.

McKnight, M.E. 1971. Natural mortality of western spruce budworm *Choristoneura occidentalis*, in Colorado. U.S. Dep. Agric., For. Serv., Rocky Mt. For. and Range Exp. Stn., Fort Collins, CO. Res. Paper RM-81.

Painter, R.H. 1966. Lessons to be learned from past experience in breeding plants for insect resistance. Pages 349-355 *in* H.D. Gerhold, E.J. Schreiner, R.E. McDermott, and J.A. Winieski, eds. Breeding pest-resistant trees. Pergamon Press, London.

Powell, J.A. 1980. Nomenclature of nearctic conifer-feeding *Choristoneura* (Lepidoptera: Tortricidae): historical review and present status. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Gen. Tech. Rep. PNW-100.

Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. Ecol. Mono. 54:429-462.

Schütte, F. 1960. Bekampfung des Eichenwicklers (*Tortrix viridana* L.) durch Verzogerung des Knospenaustriebs. Proc. Fourth Int. Cong. Crop Protection (1957)2:1329-1332.

Scudder, G.G.E. 1979. Present patterns in the fauna and flora of Canada. Pages 87-179 *in* H.V. Danks. Canada and its insect fauna. Mem. Entomol. Soc. Canada. 108.

Shepherd, R.F. 1959. Phytosociological and environmental characteristics of outbreak and non-outbreak areas of the two-year cycle spruce budworm, *Choristoneura fumiferana*. Ecology 40:608-620.

Shepherd, R.F. 1961. A comparison of the developmental rates of one and two year cycle spruce budworm. Can. Entomol. 93:764-771.

Shepherd, R.F. 1977. A classification of western Canadian defoliating forest insects by outbreak spread characteristics and habitat restriction. *In* Insect ecology. Papers presented in the A.C. Hodson Ecology Lectures. Univ. Minnesota, Agric. Sta., Tech Bull 310.

Shepherd, R.F. 1979. Comparison of the daily cycle of adult behaviour of five forest lepidoptera from Western Canada, and their response to pheromone traps. Mitteilungen der Schweizerischen Entomologischen Gesellschaft. 52:157-168.

Shepherd, R.F. 1983. A technique to study phenological interactions between Douglas-fir buds and emerging second instar western spruce budworm. Pages 17-20 *in* R.L. Talerico and M. Montgomery. Forest defoliator-host interactions: a comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Stn., Broomall, PA. Gen. Tech. Rep. NE-85.

Schultz, J.C.; Baldwin, I.T. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science 217:149-151.

Stark, R.W. 1958. Life tables for the lodgepole needle miner *Recurvaria starki* Free., (Lepidoptera: Gelechiidae). Proc. Tenth Int. Cong. Entomol. (1956) 4:151-162.

Stark, R.W. 1959. Climate in relation to winter mortality of the lodgepole needle miner, *Recurvaria starki* Free., in Canadian Rocky Mountain Parks. Can. J. Zool. 37:753-761.

Stark, R.W. 1965. Recent trends in forest entomology. Ann. Rev. Entomol. 10:303-324.

Thomson, A.J. 1979. Evaluation of key biological relationships of western budworm and its host trees. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Inf. Rep. BC-X-186.

Thomson, A.J.; Harris, J.W.E.; Silversides, R.H.; Shepherd, R.F. 1983. Effects of elevation on the rate of development of western spruce budworm (Lepidoptera: Tortricidae) in British Columbia. Can. Entomol. 115:1181-1187.

Thomson, A.J.; Shepherd, R.F.; Harris, J.W.E.; Silversides, R.H. 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae) in British Columbia. Can. Entomol. 116:375-381.

von Rudloff, E. 1972. Seasonal variation in the composition of the volatile oil of the leaves, buds, and twigs of white spruce (*Picea glauca*). Can. J. Bot. 50:1595-1603.

von Rudloff, E. 1975. Seasonal variation in the terpenes of the foliage of black spruce. Phytochemistry 14:1695-1699.

von Rudloff, E; Granat, M. 1982. Seasonal variation of the terpenes of the leaves, buds and twigs of balsam fir (*Abies balsamea*). Can. J. Bot. 60:2682-2685.

von Rudloff, E.; Rehfeldt, G.E. 1980. Chemosystematic studies in the genus *Pseudotsuga* IV. Inheritance of geographical variation in the leaf oil terpenes of Douglas-fir from the Pacific Northwest. Can. J. Bot. 58:546-556.

Volney, W.J.A. 1985. Comparative population biologies of North American spruce budworms. Pages 71-84 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Volney, W.J.A.; Waters, W.E.; Akers, R.P.; Liebhold, A.M. 1983. Variation in spring emergence patterns among western *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in southern Oregon. Can. Entomol. 115:199-209.

Wellington, W.G. 1948. Measurements of the physical environment. Canada Dept. Agric., Ottawa, Ont. Bi. Mon. Prog. Rpt. 4:1-2.

Wellington, W.G.; Fettes, J.J.; Turner, K.B.; Belyea, R.M. 1950. Physical and biological indicators of the development of outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. J. Res. D. 28:308-331.

Wulf, N.W.; Cates, R.G. (in press). Site and stand characteristics related to budworm density and tree damage. Chap. 7 *in* M.H. Brookes, R.W. Campbell, R.W. Stark, R.G. Mitchell, and J.J. Colbert, tech. coords. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1694.

Comparative Population Biologies of North American Spruce Budworms

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Patterns of variation in traits that determine population success of the spruce and western spruce budworms are compared. The two species differ little in their biologies. Geographic variation, where documented, tends to be clinal in the spruce budworm and racial in the western species. Their respective host species vary with similar patterns. Reconstructions of Holocene host-tree histories suggest that western spruce budworm hosts have migrated little compared to spruce budworm hosts. Examination of budworm life-history traits suggests that gene flow from high-elevation western populations to low-elevation eastern populations is more probable than the reverse. A model, based on the probable Holocene history of North American coniferous forests and budworm-dispersal patterns, is proposed to explain the current patterns of variation observed.

Ce document compare les variations de caractères qui déterminent le succès des populations de la tordeuse occidentale de l'épinette et de la tordeuse des bourgeons de l'épinette. Les deux espèces diffèrent peu biologiquement. Les variations géographiques, lorsqu'on les connaît, tendent à varier par degrés insensibles chez la tordeuse des bourgeons et sont plutôt raciales chez la tordeuse occidentale. Il en va de même de leurs hôtes respectifs. Les reconstructions des antécédents de leurs hôtes, à l'holocène, portent à croire que les hôtes de la tordeuse occidentale ont peu migré comparativement à ceux de la tordeuse des bourgeons. D'après l'examen des traits du cycle évolutif des tordeuses, le flux génique des populations occidentales des habitats d'altitude vers les populations orientales de basse altitude est plus probable que l'inverse. Un modèle fondé sur l'histoire probable des forêts de conifères de l'Amérique du Nord durant l'holocène et des formes de dispersion des tordeuses est proposé pour expliquer les variations actuellement observées.

Introduction

Few insect species have been scrutinized as much as members of the genus *Choristoneura*. Much work in the past 4 decades focused on two fir- and spruce-feeding species, which are among the most destructive defoliators in North America: the spruce budworm (*C. fumiferana* (Clemens)) and the western spruce budworm (*C. occidentalis* Freeman). Since McKnight's (1968) review, a significant body of literature on the biology of these species has accumulated. Much of this work, focused on life-history traits thought to be important in determining success of the insects, has documented the extreme variation (within and among populations) that is seldom subsumed by interspecific differences. The bewildering variation in characters traditionally used in establishing boundaries of taxonomic categories has hindered the development of a biologically adequate classification for the conifer-feeding members of this genus (Powell 1980).

In this paper, I assess the nature and significance of this variation in the two principal pest species of the genus and describe any patterns that emerge from this analysis. Rather than provide a list of similarities and differences, I shall use these comparisons to infer the phylogenetic relation between the species and hypothesize a mechanism to explain the patterns observed. My ultimate objective is to indicate where results may validly be extrapolated from one species to the other and caution where extrapolation may be dangerous. These conclusions will be of value as we design pest-management procedures based on techniques that depend on species-specific responses for their efficacy.

Stehr (1967a) argued for a population-biology perspective in understanding relations among budworm population size, density, quality, and dynamics. This approach synthesized the relevant information about the budworms' ecology, genetics, and evolution. Pivotal to this understanding is the concept of gamodeme: the population of interbreeding individuals limited only by the spatial and temporal boundaries of their breeding system. Establishing breeding-system boundaries is problematical and must be done experimentally, however. Despite the difficulties it presents, the solution of this problem has important practical consequences in pest management. Stehr (1967b) also recognized that the evolutionary histories of conifer-feeding *Choristoneura* would be reflected in the geological and climatological history of their hosts. This observation was tantalizingly perceptive because recent biogeographical events that could influence the evolution of this group have been extensively documented by paleontologists. Its real significance is that, although the evolutionary record of the budworm/forest system may not have a fossil record, many of these events are remarkably recent.

Maps of insect distribution and host range may be combined to delineate the known and probable spatial gamodeme boundaries of the "species" as we currently conceive them. This approach ignores any infrastructure within gamodemes occupying large areas devoid of any obvious physical barriers. The present range of *C. fumiferana* is almost continuous from the Avalon Peninsula of Newfoundland to the Mackenzie Delta on the Arctic Ocean. The range of white spruce (*Picea glauca* (Moench) Voss),[1] an important host species of the spruce budworm, extends to the Pacific at Cook Inlet and the Chukchi Sea in Alaska. Thus, if we assume that the spruce budworm follows its hosts' ranges, its distribution probably spans 100° of longitude and 25° of latitude. This is too large an area to be devoid of population structure. In contrast, the present range of *C. occidentalis*, which is associated with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests, extends from British Columbia to Arizona and probably into the Tropics in the Sierra Madre of Mexico (Stehr 1967b), spanning 25° of longitude and perhaps 35° of latitude. Although this area is much smaller, the effect of the West's physiography has been to produce forest distributions with obvious spatial boundaries that may be used to delimit the western spruce budworm gamodemes.

Temporal gamodeme boundaries are more difficult to establish. I shall limit this discussion to the Holocene epoch, which began 20,000 to 15,000 years before the present (BP). This probably marks the initial retreat of the North American ice sheets that developed in the Wisconsin glacial stage.

Holocene Biogeography of Budworm Hosts

According to Flint (1971, p. 330), at the beginning of the Holocene, the coniferous forest was shifted 20° (2 220 km [1,380 mi]) south of where it survives today. This forest spanned only 2 to 5° of latitude (140 km [120 mi.] to 550 km [350 mi.]) probably because environments suitable for its survival were "compressed" between the ice sheet and the Tropics; the Tropics has changed little in extent (Holmes 1965). Continental in climate, early Holocene boreal forests occupied a narrow belt west of the Appalachians from western Pennsylvania, through Missouri, to the east slopes of the Rocky Mountains in Montana. Bryson and Wendland (1967) show this forest in the Rocky Mountain foothills of what is now Wyoming. Although *Abies* pollen is difficult to recognize (Bakuzis and Hansen 1965), fir may have been a minor component of or absent from this forest. This view is supported by Davis's (1967) and McAndrews's (1967) reconstructions of early Holocene vegetation south of the Great Lakes. On the east coast, a maritime spruce-fir forest covered an area from what is now southern Pennsylvania to northern South Carolina, and bounded by the Appalachian Mountains to the west (Flint 1970). Fir (*Abies* sp.) was always a consistent component of this region's pollen record (Wright 1971). Forest migration northward from these refugia was determined by the rate of deglaciation and physical barriers such as the Great Lakes, Lake Agassiz, the Rockies in the West, and the Appalachians in the East. The present distribution of balsam fir is probably the result of a northerly migration from the eastern refugia into New England and a subsequent westerly spread north and south around the Great Lakes. The modern distribution of red spruce (*Picea rubens* Sarg.) suggests a similar migration route without a southern Great Lakes advance but reaching the 80° meridian. Lester (1974) provides evidence of distinct balsam fir phenotypes east and west of this meridian north of the Great Lakes. This discontinuity probably resulted from the meeting of two previously isolated populations following migrations circumventing the Lakes. My conjecture is that balsam fir was not a component of an Alaskan refugium. White spruce, in contrast, would have colonized deglaciated lands across a broad front from the continental refugium. The continental spruce-dominated forest would have established contact with the eastern spruce-fir forest east of the Great Lakes between 10 and 8,000 years BP (cf. Terasmae 1974, Fig. 10). The boreal forest reached its approximate northern limits about 6,000 years BP (Nichols 1975). Balsam fir pollen appears in the stratigraphic record at 115° W longitude 2,000 to 3,000 years BP (Nichols 1975, Fig. 1), suggesting a probable date when it reached the western limits of its range.

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[1] Throughout, host ranges are from Little (1971).

The western situation is complicated because more host species are involved and the stratigraphic record is not as complete as it is in the East. The Wisconsin Cordilleran ice sheet in western North America extended from central Alaska south to northern Washington and was continuous from the Pacific east to the Laurentide ice sheet, which it met in the foothills of the Rocky Mountains (Flint 1970). South of this front, in the mountain and Pacific states, alpine glaciers formed; their altitudinal extent depended on topography, latitude, and distance inland. Evidence from the location of cirques suggests that these glaciers may have extended down to 610 m (2,000 ft) in the northern Cascades, 1 830 m (6,000 ft) in the southern Cascades, and 2 240 m (8,000 ft) in the Sierra Nevada; in the Rockies they were at 1 830 m (6,000 ft) in the Inland Empire, and 3 660 m (12,000 ft) in northern New Mexico (Flint 1970, Fig. 18-4). As a consequence, Canada was devoid of vegetation and western forests in the United States survived at lower elevations and south of their present range. Interpretation of macrofossil evidence places these early Holocene forests about 450 km (280 mi.) south and 800 m (3,000 ft) downslope from their modern counterparts in Arizona and Utah (Cole 1982). Except for the destruction of the northern forests, forest types susceptible to the western spruce budworm expanded during the late Wisconsin age, particularly in the southern latitudes, because of this downslope migration and the more favorable climatic conditions prevailing (Flint 1970, Figs. 19-3, 16-2; Martin and Mehringer 1965).

A major biogeographical event resulting from the glacial advance into the Pacific Northwest was that Douglas-fir populations were split into what are now recognized as the coastal variety *menziesii* and the inland variety *glauca*. Just before this, Douglas-fir went through a period of explosive population growth, variously attributed to the evolution of a new karyotype or climatic change after the last pluvial period (Silen 1978). A period of rapid population growth and range expansion after deglaciation has been documented by Tsukada (1982), who concluded that contact between the two varieties was re-established some 7,000 years BP.

Associated with Douglas-fir and major hosts of the western spruce budworm are several species of true firs, spruces, and larches. The principal fir associate in the Cascade and coastal forests is grand fir (*A. grandis* (Dougl.) Lindl.) in the northern Cascades, white fir (*A. concolor* (Gord. & Glend.) Lindl. var. *lowiana*) in the southern Cascades, depending on elevation: grand fir and subalpine fir (*A. lasiocarpa* (Hook.) Nutt.) in the Canadian Rockies and adjacent states; and subalpine fir, cork bark fir (*A. lasiocarpa* var. *arizonica*), and white fir (*A. concolor* var. *concolor*), in the Southwest. Engelmann spruce (*Picea engelmannii* Parry) is a component of these forests in the northern Cascades and Rocky Mountains, and Colorado blue spruce (*P. pungens* Engelm.) is present in the southern Rockies. White spruce is present within the range of the western spruce budworm at the Alberta–British Columbia/Montana borders. Depending on elevation, western larch (*Larix occidentalis* Nutt.) and subalpine larch (*L. lyallii* Parl.) are also components of these forests in the northern Cascades, the northern Rocky Mountain states, and adjacent Canada. Macrofossil evidence from the Southwest suggests that these associations may have been in a state of flux for most of the period under consideration (Cole 1982; Mehringer and Ferguson 1969). Individual host-tree reaction to climatic change determined the details of forest composition, but the host species of this region may have remained unchanged for as long as 300,000 years (Barnosky 1984).

Host Relations

Marked differences occur in the patterns of geographic variation among the two budworms' host-tree species. In the East, the gentle topography and increasingly drier and cooler conditions to the west are correlated with east/west clines (Table 1). By contrast, race formation has been prevalent among the western species (Table 1), perhaps because of the patchy distribution of suitable habitats. White spruce, a boreal species, possesses an east/west cline stretching from Newfoundland to the MacKenzie and Richardson Mountains in the west. This is also the eastern boundary of the Alaskan race of white spruce. Where the ranges of similar eastern and western host species overlap, introgression is always evident (Table 1). Similarly, introgression is common among the host species of the western spruce budworm. In general, eastern and western host species have not differentiated sufficiently to become reproductively isolated. Thus, in addition to their spatial overlap, much overlap occurs in biological traits between eastern and western host species of these budworms.

Nevertheless, real genetic and developmental differences among neighboring western forest stands further complicate the patterns in host-tree variation. Thus, racial (Steiner 1979) and intertree differences (Beckwith and Kemp 1984) in the time of budburst for interior Douglas-fir contribute significantly to local variation. Similarly, genetic variation in the phenology of coastal Douglas-fir populations is associated with elevation, aspect, and distance of the provenance from the ocean (Sorensen 1983). The distances may be small: significant three-dimensional clinal variation in growth characteristics of coastal Douglas-fir populations were detected by Silen and Mandel (1983) over distances as short as 16 km (10 mi.) and elevational differences of only 310 m (1,000 ft).

Table 1
Geographic variation in budworm host-tree species

Host species	Species code	Range	Pattern of variation	Introgresses with	References[1]
Principal spruce budworm hosts:					
Abies balsamea	1	Eastern	E/W cline	7	a
Picea glauca	2	Boreal	E/W cline[2]	8	a,b
P. mariana	3	Boreal	None	4	a
P. rubens	4	Eastern	None	3	a
Principal western spruce budworm hosts:					
Abies concolor	5	Western	2 races	6	b
A. grandis	6	Western	5 races	5	b
A. lasiocarpa	7	Western	2 races	1	b
Picea engelmannii	8	Western	Unknown	2,9	a
P. pungens	9	Western	Unknown	8	b
Pseudotsuga menziesii	10	Western	9 races	—	c

[1] a = von Rudloff (1975), b = Fowells (1965), c = Wright et al. (1971)
[2] Alaskan race also

Several other sources of local variation are evident at many hierarchical levels — every one bearing its own peculiar seasonal and annual pattern. Within a stand, species composition, trees, and crown and canopy levels are recognized as contributing significantly to the variability in habitat characters that are important to the budworm. Shoot phenology, bud production, shoot growth and concomitant changes in the nutritional value of host tissues, and the production of secondary compounds are all known to be subject to these sources of variation. Each of these phenotypic traits have special significance in determining budworm success.

Host phenology is known to vary with respect to budworm development. This asynchrony affects budworm survival on balsam fir (Eidt and Cameron 1973) and has been identified as a correlate with the occurrence of western spruce budworm outbreaks in British Columbia (Thomson et al. 1984). Experiments in New Brunswick showed that phenological differences among white, grand, and balsam firs were not sufficient to interfere with spruce budworm development (Eidt and MacGillivray 1972). Cameron et al. (1968) found good synchrony between spruce budworm development and balsam fir shoot growth in New Brunswick. Blais (1957) and Greenbank (1963a) suggested that phenological differences between black spruce and the other host species were sufficient to explain the different patterns of budworm survival and damage among the two sets of host species. These differences may be caused by microclimatic differences among sites rather than genetic differences among hosts. Manley and Fowler (1969) found phenological differences among black spruce, red spruce, and their hybrids to be negligible. Bean and Wilson (1964) found that accumulated degree-days were a better predictor of budworm development than balsam fir shoot growth. Apparently, cues that initiate budburst are different from those that induce budworm development. Kemp and Beckwith[2] found significant annual variation in the degree-day date of budburst for both Douglas-fir and grand fir in western sites. They pointed out that, although soil temperature regimes determined the date of budburst in Douglas-fir (Cleary and Waring 1969), accumulated degree-days based on effective air temperatures determined western spruce budworm emergence in the spring. No differences were detected among parameters for budworm development in the different budworm gamodemes studied by Cameron et al. (1968) in New Brunswick, Wagg (1958) in Orgeon, and other Pacific Northwest sites (Beckwith and Kemp 1984).

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[2] W.P. Kemp, Dept. For. Res., Univ. Idaho, Moscow, Id. and R.C. Beckwith, U.S. Forest Service, Corvallis, OR, personal communication.

Much of the differences reported among species and regions may thus be explained by differences in the local environments rather than by genetic differences among gamodemes of budworm or their hosts.

Variation in host-tree phenology and the dependence on environmental cues other than those that affect the tree in initiating budburst make the spring emergence of the budworm hazardous. Overcoming the hazard of feeding-site establishment in the spring is accomplished by variation in feeding habits depending on the availability of suitable buds.

Both the spruce budworm (Thomas 1976) and the western spruce budworm (Volney et al. 1983) have protracted periods of spring emergence. The distributions of emergence times are adequately modeled by the lognormal distribution. In western spruce budworm populations, the variation is such that the variance within a family (offspring from a single female) is almost that of the population variance (Volney et al. 1983). Such a pattern is effective in spreading the risk of early-instar mortality resulting from failure to establish feeding sites. When host-tissue availability is variable and unpredictable, this pattern allows all families to be represented among individuals emerging synchronously with bud development. Thus, all families can react to the range of spring conditions experienced by the populations, and opportunity is limited for selection to reduce variation that is not associated with spring emergence time.

More significantly, perhaps, is the effect of host-tree flowering on this process. The occurrence of flowering before vegetative budburst expands the phenological window for budworm feeding-site establishment (and survival) considerably. Because the distribution of spring emergence times is skewed to the left, the expansion of the phenological window early in the season can result in more than a proportionate increase in budworm survival. Conditions associated with flowering of balsam fir are associated with elevated survival of early instars (Blais 1952; Greenbank 1963a). Although his evidence was derived from outbreak populations, Blais believed that flower production in balsam fir and elevated early-instar survival was one mechanism responsible for the release of spruce budworm populations.

Production strategies in host-tree buds can thus affect budworm survival. The spruces and Douglas-fir, which are less shade-tolerant than the firs, produce both microsporangiate and megasporangiate strobili throughout much of their crowns (Fowells 1965). In Douglas-fir, reproductive buds are known to be produced in the unshaded portions of the crown (Silen 1973). Balsam fir (Powell 1977) and other true firs (Fowells 1965) have a distinct megasporangiate zone at the crown apex immediately above a narrow microsporangiate zone, also in the upper crown. Although the number of vegetative buds per unit branch area may not differ significantly among eastern host species (Greenbank 1963b), the number of reproductive buds per tree on the more shade-tolerant fir is probably substantially lower. The importance of bud dynamics in budworm population release was not addressed in much of the subsequent work, which continued to focus on outbreak populations.

Latent-bud production may be a factor that influences the duration of outbreaks. Douglas-fir and the spruces produce latent buds on their shoots for most of their lives. These buds are stimulated after defoliation and a second crop of buds will be produced after feeding is complete. Consequently, the size of the bud population increases for several years during an outbreak. This process may prolong the period over which outbreaks are sustained by these hosts. Balsam fir (Batzer 1973) and white fir, by contrast, lose this ability early in their lives. Only the ability of the young trees to sprout adventitiously allows the true firs to survive outbreaks.

Greenbank (1963b) considered white spruce shoot growth, which is significantly greater than in fir, another means by which white spruce sustains defoliation longer than balsam fir. Similarly in the West, Douglas-fir can sustain more defoliation (Carolin and Coulter 1975), and its shoot growth is greater than in grand fir (Beckwith and Kemp 1984). Both species of spruce budworm are apparently similar in ability for damaging the shade-tolerant true fir component of their host stands more than the less shade-tolerant spruces and Douglas-fir.

Evaluating host preferences and suitability is difficult. An understanding of several processes, ranging from stimuli that initiate and maintain feeding to the influence of host tissue on fitness, is required to assess a true preference. Experiments have clearly shown that all four major host plants of the spruce budworm present adequate feeding stimuli (Albert 1983; Albert and Parisella 1983). Detailed work of this nature has not been done on the western species, but because Douglas-fir, spruces, firs, and even larches are fed on extensively (Fellin and Dewey 1982), the assumption that they all have phagostimulants — which function in initiating and maintaining feeding by the western spruce budworm — is reasonable.

Food quality, represented by the various host tissues used, influences budworm productivity. Caloric intake and caloric intake per milligram of protein consumed are correlated with spruce budworm survival, developmental rate, and pupal weights. Pupal weights are correlated with F_1 survival (Shaw et al. 1978). These indexes are used because several nutritional components interact in as yet unknown ways to determine budworm performance. Nutritional components include sugars (Harvey 1974), crude fat, protein (correlated with total nitrogen in the diet), and moisture content

(Shaw et al. 1978). All these components vary annually, seasonally, and locally, but not significantly among plots separated by 224 km (139 mi.) (Shaw and Little 1977) in New Brunswick. Mattson et al. (1983) obtained similar results for spruce budworm reared on all major hosts found in Minnesota. They also found that pupae derived from larvae reared on balsam fir and upland black spruce were larger than those from white and lowland black spruces. Thomas (1983), however, obtained heavier pupae from white spruce than from balsam fir. These discrepancies indicate the nature of variation that might be expected to be induced by the complex interaction of biotic and abiotic factors that determine food quality in the several hosts of the spruce budworm. Further, food quality can be manipulated through fertilizer treatments. Thus, over a range of 8.8 to 17 percent foliar nitrogen in trees treated with inorganic fertilizers, female pupal weights generally increased in spruce budworm reared on balsam fir trees in New Brunswick (Shaw et al. 1978).

Similarly, over a broad range of foliar nitrogen concentration, both white fir and Douglas-fir are adequate hosts for the western species; only at uncommonly high or low concentrations were deleterious effects detected (Brewer et al., in press). In the Southwest, the western spruce budworm developed faster on Douglas-fir than on either white or cork bark firs, but no effect was found in pupal weights (Wagner and Blake 1983). Beckwith (1983) found Douglas-fir and Engelmann spruce to be slightly better hosts than subalpine fir, but western larch — although fed on by larvae — was distinctly inferior. Thus, the cues that initiate and sustain feeding are not always associated with nutritionally superior hosts. Western spruce budworm growth rates also differ among populations, and they are altered by extreme concentrations of nitrogen, bornyl acetate, and beta pinene incorporated in artificial diets (Cates et al.[3]). These experiments also demonstrated that each population of the western spruce budworm reacted in its own way to the variable dietary components; significant two-factor interactions occurred between nitrogen and terpenes to influence growth rates; and survival was determined by concentrations of nitrogen and bornyl acetate. Thus, terpenes may interact with nutritional components to influence budworm success, but, terpene concentration is known to vary geographically, annually, seasonally, and locally in all budworm hosts that have been examined (von Rudloff 1975). It is not surprising, therefore, that the budworms are extremely tolerant of large differences in food quality.

Life-History Traits

To be successful, an organism must feed, grow, mate, reproduce, and avoid natural enemies. Success sometimes involves dispersal induced by environmental modifications of commonly observed behavior (Wellington 1980). Species comparisons would be most successful if matrices containing correlations of life-history traits — obtained under identical conditions — could be contrasted. Unfortunately, this has never been done for spruce and western spruce budworms; consequently, individual traits must be compared one at a time.

Fecundity is often used as a measure of population success, but it is subject to considerable environmental control. Potential fecundity (Thomas et al. 1980) of field populations, while variable, does not differ between the two species (Table 2). On average, dead spruce budworm females found in the field have laid 70 to 80 percent of their potential egg complement; populations seldom realize their full potential (Thomas et al. 1980). No comparable data are available for the western spruce budworm, but they are also unlikely to lay their full egg complement in nature. Because the full egg complement is seldom deposited in their native stands, egg-deposition rates and variation in egg quality associated with deposition order must be recognized as traits that can influence population success in these species. Egg-deposition rates of the western spruce budworm have not been studied in detail, which makes comparisons impossible. Harvey (1977), however, has shown that, in the spruce budworm, mean egg weight declines with deposition order, that individuals from the latter half of eggs deposited emerge later, survive to the second instar better, and more females occur among them than in the first half. An east/west cline has been demonstrated in the mean egg weight of the first eggs laid (Harvey 1983a), which is largely unchanged by variations in temperature and diet, and its heritability is high (Harvey 1983b) and thus susceptible to rapid selection. Harvey (1983b) suggests that the heavier eggs in western populations of the spruce budworm endow larvae with greater food reserves, which allows survival over the longer western winters.

Some measures have been made of initial mean egg weights of the western spruce budworm that permit comparison. Harvey (1983b) found the mean initial egg weights on one of the western spruce budworm populations (Montana) and a spruce budworm population (Ontario) to be 0.182 and 0.161 mg, respectively. Based on the relation between latitude and mean initial egg weight, the Montana estimate is anomalously high and corresponds to a latitude 7° north of the insects' origin. Other estimates of mean initial egg weights have not been determined for the western spruce budworm. Data from Brewer et al. (in press) allows estimation of the mean initial egg weights of the western spruce

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[3] R.G. Cates, C. Henderson, and R.R. Redak, Dept. Biology, Univ. New Mexico, Albuquerque, NM, personal communication.

Table 2
Mean field fecundity of the spruce budworm (SB) and the western spruce budworm (WSB)

Species	Locale	Mean	Reference
SB	Ontario	195.3	Harvey (1983b)
SB	NW New Brunswick	162-209	Miller (1963)
SB	NW Ontario	157-182	Blais (1953)
SB	New Brunswick	201-255	Thomas et al. (1980)
WSB	Colorado	154.4	McKnight (1971)
WSB	SW Oregon	125-237	Volney et al. (1984)
WSB	New Mexico	159-215	Volney (unpubl.)
WSB	Pacific Northwest	100-200	Campbell (in press)

budworm. The mean weight of eggs produced by females, which laid only a small number of eggs in these experiments may be assumed to approach Harvey's initial egg weight. These values range from 0.164 to 0.174 mg, suggesting an origin at least 3 to 4° north of where the insects used in the experiment were originally collected. Such comparisons confound species effects with elevational effects in the place of origin; nevertheless, they suggest that western spruce budworm populations from higher elevations produce larger eggs in the first masses than their spruce budworm counterparts from the same latitude but at lower elevations and further east.

Diapause synchronizes development after hatching in both species. Some populations live in environments where development is not completed in a single growing season. Some budworm populations are adapted to this condition by being able to enter a second diapause. The two-year-cycle budworm (*C. biennis* Freeman) is distinguished from the spruce budworm and the western spruce budworm by the high incidence of a second diapause. In several respects, the two-year-cycle budworm is intermediate to the other two. A second diapause in the spruce budworm and the western spruce budworm is variable and subject to artificial manipulation, however (Harvey 1967). This may be a character that shows clinal variation in response to increasing elevation, latitude, or both.

Growth rates differ among species in detail only. The median postdiapause development time is shorter in the spruce budworm than in any of the four fir- and spruce-feeding budworms of North America (Stehr 1964). In addition, other studies show that development time varies little in the different populations of the spruce budworm and the western spruce budworm (Table 3). Despite these differences, a substantial degree of overlap in development times remains among the species (cf. Stehr 1964), but the spruce budworm population is more variable than any of the others examined. The general pattern of postdiapause development does not differ between species. For the western spruce budworm, no detectable difference in development between the sexes has been found up to the end of the fifth instar; females spend a substantially longer time in the sixth instar than males, but their pupal stadia are only slightly shorter. Thus males eclose before females.[4] Similarly, spruce budworm females spend a shorter time in the pupal stage (Sanders 1975), but are preceded by males at eclosion by 1 to 2 days (Stehr 1964). Clearly, the two species would react the same to a given environment and would not be seasonally isolated should they become sympatric.

Slight differences in the daily patterns of mating activity have been observed. Half the spruce budworm females maintained at 20°C on a 17-h photoperiod began calling 3½ to 4½ hours before lights were turned out (Sanders 1971a; Sanders and Lucuik 1972), but

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[4] W.J.A. Volney and A.M. Liebhold, Dept. Entomological Sciences, Univ. California, Berkeley, CA, Unpublished data.

Table 3
Median postdiapause development times

Species	Rearing temperature (°C)	Development time		Reference
		Females	Males	
C. fumiferana	Unspecified	29.5	26.5	Stehr (1964)
C. occidentalis	Unspecified	32.5	29.5	Stehr (1964)
C. retiniana	Unspecified	37.5	30.8	Stehr (1964)
C. occidentalis	25	34.4	32.2	Volney and Liebhold[a]
C. retiniana	25	36.8	33.9	Volney and Liebhold[a]
C. fumiferana[b]	21	29.0	27.5	Harvey (1975)
C. occidentalis[b]	23-26	29.5	29.5	Lyon et al. (1972)[c]

[a] Unpublished data.
[b] Mean.
[c] Insects not sexed.

western spruce budworm females did not react similarly until 2 h before lights out (Liebhold and Volney, 1984). The spruce budworm is intermediate between the western spruce budworm and the two-year-cycle budworm (Sanders et al. 1977). Both spruce budworm and western spruce budworm females begin calling earlier at lower temperatures (Leibhold and Volney 1984; Sanders and Lucuik 1972). The circadian periodicity of this behavior in the western spruce budworm can be modified by selection (Liebhold and Volney 1984). In general, the diel distribution of male response to artificial attractants is similar to the distribution of female calling, except that it is less protracted.

Where they have been tested in the field, the two species are cross attractive (Sanders et al. 1977) and laboratory bioassays support this conclusion (Sanders 1971b). The two species share the same major pheromone components (Sanders and Weatherston 1976; Silk et al. 1982). The response of spruce budworm males to western spruce budworm females is only half of what it is to conspecific females, however, which suggests subtle differences in the pheromone chemistry of the two species. Silk et al. (1982) attribute this to detectable quantities of E/Z 11-tetradecenyl acetate and E/Z 11-tetradecanol mixed with the principal pheromone components (E/Z 11-tetradecenal) in western spruce budworm virgin-female effluvia. The function of the minor components in long-range attraction of conspecific western spruce budworm males to females is unknown (Cory et al. 1982). Whatever the reason, cross-attraction is asymmetric; matings between spruce budworm males and western spruce budworm females occurs less frequently than the reciprocal cross, but this degree of incompatibility is unlikely to be significant in preventing interspecific matings in nature.

Both species are dispersed as larvae (Beckwith and Burnell 1982; Régnière and Fletcher 1983). Whether this results in significant long-range (>100 km, 62 mi.) dispersal is unknown, but this process is important in redistributing insects within stands and may be exploited in silvicultural control (Jennings et al. 1983). Adult dispersal is significant in moving insects over great distances. In dense populations, spruce budworm females make vertical flights after laying a variable portion of their eggs. This behavior may be repeated nightly under the appropriate environmental conditions (Greenbank et al. 1980). Moths have been recovered as far as 450 km (280 mi.) from their native stand in a single night of nonstop flight (Dobesberger et al. 1983). Flight capacities reported by Greenbank et al. (1980) suggest an upper limit of 800 km (497 mi.) for moths in a single night. Although long-range dispersal of the western spruce budworm has not been documented in such detail, massive moth flights associated with storms have been reported on several occasions in British Columbia and the adjacent states (Carolin, in press).

Synthesis

An examination of all life-history traits studied in detail so far suggests that no barriers exist to gene flow between the two species. Variability within and among host trees is sufficient that variability in host quality among locations is comparatively trivial over distances at least as great as 225 km (140 mi.) for the spruce budworm.

Ample evidence exists that local and geographic variation in host traits are matched by an impressive array of variable life-history traits, allowing each budworm species to thrive in its own habitat. With the patterns of host-species variation described above, one would expect each species to be capable of colonizing the other's hosts. Not surprisingly, Harvey (1983b) reared western spruce budworm larvae on balsam fir foliage, and the spruce budworm does well on western firs (Eidt and MacGillivray 1972). The two host-tree groups are not sufficiently distinct to present much of a barrier to gene flow between the two insect species.

Deficiencies in food quality, if they are relatively small, are ameliorated by two physiological mechanisms that tend to buffer population changes. Development time is often extended on marginally inferior host trees and female pupae are produced as heavy as those from slightly better hosts. Slight deficiencies in host quality are thus overcome by what appears to be compensatory feeding in both insect species. The second mechanism produces eggs of almost uniform size in the first egg masses laid regardless of the female's nutritional history. Although fecundity can be altered by varying food quality, mean initial egg weights are almost completely under genetic control (Harvey 1983b). This control effectively buffers eggs from the vicissitudes of the female's environment. Furthermore, dispersal flights are often made only after the first eggs have been laid (Greenbank et al. 1980). If egg size is associated with overwinter survival and the optimum egg size varies clinally (Harvey 1983a), this peculiar combination of dispersal and oviposition traits ensures that locally adapted progeny are left in the egg-laying female's native stands. The consequences of smaller mean egg sizes and higher proportion of females among the last laid eggs carried by dispersing females are discussed below.

Neither species has distinctive life-history traits or host requirements that would preclude their establishment within the other's range. All critical life-history traits examined so far are plastic, may be changed rapidly by selection, or are variable and inherited so that variation is conserved. Were detection possible (no suitable characters distinguish the species), the two species would doubtless hybridize in nature where they occur sympatrically. This assumption is based on the observation that some sympatric populations of *C. occidentalis* and *C. retiniana*, which are only marginally cross-attractive (Liebhold et al. 1984), successfully hybridize in nature and produce viable offspring (Volney et al. 1984).

Attempts to establish an evolutionary relation between these species are frustrated by a lack of suitable fossil evidence. That they are close phylogenetically is suggested by the extreme patterns of within — relative to among — species variation. Further, isozyme analyses show the remarkable similarities among all conifer-feeding *Choristoneura* species (Harvey 1985). By combining information on their biology with modern climatological and vegetation patterns, we can reconstruct prehistoric environmental patterns to arrive at reasonable conjectures as to the course of their evolution.

Gene flow would be effected by adult dispersal and reproduction. After dispersal, two routes are possible to successful budworm establishment in distant stands. Either colonizing males would have to mate with local females, or the eggs deposited by migrating females would have to survive. Except for seasonal differences between the source and the destination, western spruce budworm males would be more likely to be successful in mating with spruce budworm females than the reverse cross because of the asymmetry in cross-attractiveness. The larger eggs transported by western spruce budworm females from populations at higher elevation would be laid in milder winter environments at the lower elevation of eastern destinations. If Harvey's (1983a) conjecture is right, the larger eggs of the western spruce budworm have a better chance of surviving in the East than those of spruce budworm moved to the West. Both routes to gene flow favor a west-to-east flow between populations.

Both species are transported by storm systems (Carolin, in press; Greenbank et al. 1980). Current circulation patterns in North America track from west to east (Wellington 1954). Paleoclimatic reconstructions (Bryson and Wendland 1967) suggest that Holocene changes in these patterns would also have transported moths from the montane coniferous forest to the western boreal forest. The source populations in the Rockies, however, would have changed as the location of the boreal forest changed in latitude with climatic fluctuations. The biological and physiographic evidence thus suggest that gene flow would be adequately described by a riparian model with a western source, at high elevation, in which colonists are driven east/northeast by the prevailing circulation patterns. Today, movements are probably between *C. biennis* and *C. fumiferana* in the northern Rocky Mountains. Migration in the opposite direction, although possible, would be less likely to be successful in effecting gene flow.

The absence of a fossil record cannot be used as evidence for the recency of the association between the insects and their hosts (for a variety of reasons, the recent North American lepidopteran fossils are poorly known [Howden 1975]). Several other lines of evidence support — or, at least, are not at odds with — the hypothesized model, however.

The results of isozyme studies reported by Stock and Castrovillo (1981) and Harvey (1985) indicate that distance, rather than substantial differences in biological traits, is a better indicator of isozyme-related genetic difference among taxa. Western pine-feeding and fir- and spruce-feeding *Choristoneura* live in sufficiently similar environments or sufficient genetic exchange occurs between them to produce isozyme patterns that make them very dissimilar from the spruce budworm populations from Maine. The western spruce budworm populations tend to be highly variable genetically (Willhite and Stock 1983). Such a pattern probably results from a selection for locally adapted populations coupled with occasional environmental impediments to successful gene flow under current climatic and biotic conditions within their range. The development of clines in a few isozyme frequencies and apparently patternless variation in others of the spruce budworm (Harvey[5]) are not inconsistent with the model of combined gene flow and selection. Finally, repeated infusion of western genes from several genetically distinct sources would explain the larger variance in certain biological traits of the spruce budworm populations than those in the West. In a sense, the eastern gamodeme has become the estuary of the North American budworm genetic river.

Although eastern maritime coniferous forests of the early Holocene may have had a budworm population, the current behavior of populations in the modern forest (Blais 1985) suggests that the association is relatively new (Stehr 1964). The western spruce budworm also fluctuates in density (Shepherd, 1985), but chronic problems with this insect seem to be restricted to regions where the forest has become re-established on recently deglaciated lands. The reconstructions presented here suggest that the budworm-forest association may be only 8,000 to 10,000 years old in eastern North America and 7,000 years in the Pacific Northwest and adjacent Canada. From the meager records available, the Douglas-fir forests on the west side of the southern Cascades and the adjacent coastal ranges in California and Oregon — which remained unglaciated — do not seem to sustain protracted budworm outbreaks. This region, with its variation in physiography and biotic communities, may provide the setting in which to test our theories on budworm population biology.

Literature Cited

Albert, P.J. 1983. Host plant preferences in larvae of the eastern spruce budworm, *Choristoneura fumiferana*. Pages 19-24 *in* Proc. 5th Int. Symp. Insect-plant relationships, Wageningen; 1982. Pudoc, Wageningen, Netherlands.

Albert, P.J.; Parisella, S. 1983. Chemical basis for host plant selection by eastern spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Pages 41-44 *in* Proc. Forest defoliator – host interactions: a comparison between the gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-85.

Bakuzis, E.V.; Hansen, H.L. 1965. Balsam fir: a monographic review. Univ. Minn. Press, Minneapolis, Minn.

Barnosky, C.W. 1984. Late Miocene vegetational and climatic variations inferred from a pollen record in northwest Wyoming. Science 223:49-51.

Batzer, H.O. 1973. Defoliation by the spruce budworm stimulates epicormic shoots on balsam fir. Environ. Entomol. 2:727-728.

Bean, J.L.; Wilson, L.F. 1964. Comparing various methods of predicting development of the spruce budworm, *Choristoneura fumiferana*, in northern Minnesota. J. Econ. Entomol. 57:925-928.

Beckwith, R.C. 1983. Western larch as a host of the western spruce budworm: a comparison of caged larvae on susceptible conifers. Pages 21-23 *in* Proc. Forest defoliator – host interactions: a comparison between the gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-85.

Beckwith, R.C.; Burnell, R.G. 1982. Spring larval dispersal of the western spruce budworm (Lepidoptera: Tortricidae) in north-central Washington. Environ. Entomol. 11:828-832.

Beckwith, R.C.; Kemp, W.P. 1984. Shoot-growth models for Douglas-fir and grand fir. For. Sci. 30(3):743-746.

Blais, J.R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana* Clem.) to the flowering condition of balsam fir (*Abies balsamea* (L.) Mill.). Can. J. Zool. 39:1-29.

Blais, J.R. 1953. Effects of the destruction of the current year's foliage of balsam fir on the fecundity and habits of flight of the spruce budworm. Can. Entomol. 85:446-448.

Blais, J.R. 1957. Some relationships of the spruce budworm, *Choristoneura fumiferana* (Clem.), to black spruce, *Picea mariana* (Moench) Voss. For. Chron. 33:364-372.

Blais, J.R. 1985. The ecology of the eastern spruce budworm: a review and discussion. Pages 49-59 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept. 84. Bangor, ME. Can. For. Serv., Ottawa, Ont.

---

[5] Harvey, B.T. 1982. Genetic variation in *Choristoneura fumiferana*. Paper presented at joint meetings of Entomol. Soc. Am., Can., Ontario. Toronto.

Brewer, J.W.; Capinera, J.L.; Deshon, R.E.; Walmsley, M.L. (In press). Influence of foliar nitrogen levels on survival, development, and reproduction of western spruce budworm, *Choristoneura occidentalis* Freeman. Can. Entomol.

Bryson, R.A.; Wendland, W.M. 1967. Tentative climatic patterns for some late glacial and post-glacial episodes in central North America. Pages 271-298 *in* W.J. Mayer-Oakes, ed. Life, land and water. Univ. Manitoba Press, Winnipeg, Manitoba.

Cameron, D.G.; McDougall, G.A.; Bennett, C.W. 1968. Relation of spruce budworm development and balsam fir shoot growth to heat units. J. Econ. Entomol. 61:857-858.

Campbell, R.W. (In press). Population dynamics. Chapter 6 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, eds. Western spruce budworm. U.S. Dep. Agric., Washington, D.C. Tech. Bull. 1694.

Carolin, V.M. (In press). Life history and behavior. Chapter 3 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, eds. Western spruce budworm. U.S. Dep. Agric., Washington, D.C. Tech. Bull. 1694.

Carolin, V.M.; Coulter, W.K. 1975. Comparison of western spruce budworm populations and damage on grand fir and Douglas-fir trees. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-195.

Cleary, B.D.; Waring, R.H. 1969. Temperature: collection of data and its analysis for the interpretation of plant growth and distribution. Can. J. Bot. 47:167-173.

Cole, K. 1982. Late Quaternary zonation of vegetation in the eastern Grand Canyon. Science 217:1142-1145.

Cory, H.T.; Daterman, G.E.; Daves, G.D., Jr.; Sower, L.L.; Shepherd, R.F.; Sanders, C.J. 1982. Chemistry and field evaluation of the sex pheromone of western spruce budworm, *Choristoneura occidentalis* Freeman. J. Chem. Ecol. 8:339-350.

Davis, M.B. 1967. Late-glacial climate in northern United States: a comparison of New England and the Great Lakes region. Pages 11-43 *in* E.J. Cushing and H.E. Wright, Jr., eds. Quaternary paleoecology. Yale Univ. Press, New Haven, Conn.

Dobesberger, E.J.; Lim, K.P.; Raske, A.G. 1983. Spruce budworm (Lepidoptera: Tortricidae) moth flights from New Brunswick to Newfoundland. Can. Entomol. 115:1641-1645.

Eidt, D.C.; Cameron, M.D. 1973. Effect of cold treatment on post-diapause spruce budworms. Can. For. Serv., Ottawa. Bi-Mon. Res. Notes 29:11-12.

Eidt, D.C.; MacGillivray, H.G. 1972. Resistance of seven fir species to spruce budworm and other insects. Can. For. Serv., Ottawa. Bi-Mon. Res. Notes 28:2-3.

Fellin, D.G.; Dewey, D.E. 1982. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. For. Insect and Dis. Leafl. 53.

Flint, R.F. 1970. Glacial and Quaternary geology. John Wiley & Sons Inc., New York.

Flint, R.F. 1971. The earth and its history. W.W. Norton & Company Inc., New York.

Fowells, H.A. 1965. Silvics of forest trees of the United States. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 271.

Greenbank, D.O. 1963a. Staminate flowers and the spruce budworm. Pages 202-218 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Greenbank, D.O. 1963b. Host species and the spruce budworm. Pages 219-223 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Greenbank, D.O.; Schaefer, G.W.; Rainey, R.C. 1980. Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. Mem. Entomol. Soc. Can. 110.

Harvey, G.T. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. V. Second diapause as a species character. Can. Entomol. 99:486-503.

Harvey, G.T. 1974. Nutritional studies of eastern spruce budworm (Lepidoptera: Tortricidae). I. Soluble sugars. Can. Entomol. 106:353-365.

Harvey, G.T. 1975. Nutritional studies of eastern spruce budworm (Lepidoptera: Tortricidae). II. Starches. Can. Entomol. 107:717-728.

Harvey, G.T. 1977. Mean weight and rearing performance of successive egg clusters of eastern spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 109:487-496.

Harvey, G.T. 1983a. A geographical cline in egg weights in *Choristoneura fumiferana* (Lepidoptera: Tortricidae) and its significance in population dynamics. Can. Entomol. 115:1103-1108.

Harvey, G.T. 1983b. Environmental and genetic effects on mean egg weight in spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 115:1109-1117.

Harvey, G.T. 1985. The taxonomy of the coniferophagous *Choristoneura* (Lepidoptera: Tortricidae): A review. Pages 16-48 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept. 1984. Bangor, ME. Can. For. Serv., Ottawa, Ont.

Holmes, A. 1965. Principles of physical geology. Thomas Nelson and Sons Ltd., London, England.

Howden, H.F. 1975. Late Quaternary history of some maritime insects. *In* J.G. Ogden III and M.J. Harvey, eds. Environmental change in the maritimes. Proc. N.S. Inst. Sci. Suppl. 3:61-65.

Jennings, D.T.; Houseweart, M.W.; Dimond, J.B. 1983. Dispersal losses of early-instar spruce budworm (Lepidoptera: Tortricidae) larvae in strip clearcut and dense spruce-fir forests of Maine. Environ. Entomol. 12:1787-1792.

Lester, D.T. 1974. Geographic variation in leaf and twig monoterpenes of balsam fir. Can. J. For. Res. 4:55-60.

Liebhold, A.M.; Volney, W.J.A. 1984. Effect of temporal factors on reproductive isolation between *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae). Can. Entomol. 116:991-1005.

Liebhold, A.M.; Volney, W.J.A.; Waters, W.E. 1984. Evaluation of cross-attraction between sympatric *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae) populations in south-central Oregon. Can. Entomol. 116:827-840.

Little, E.L., Jr. 1971. Atlas of United States trees. I. Conifers and important hardwoods. U.S. Dep. Agric., For. Serv., Washington, D.C. Misc. Publ. 1146.

Lyon, R.L.; Richmond, C.E.; Robertson, J.L.; Lucas, B.A. 1972. Rearing diapause and diapause-free western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae) on an artificial diet. Can. Entomol. 104:417-426.

Manley, S.A.M.; Fowler, D.P. 1969. Spruce budworm defoliation in relation to introgression in red and black spruce. For. Sci. 15:365-366.

Martin, P.S.; Mehringer, P.J., Jr. 1965. Pleistocene pollen analysis and biogeography of the Southwest. Pages 433-451 *in* H.E. Wright and D.G. Frey, eds. The Quaternary of the United States. Princeton Univ. Press, Princeton, N.J.

Mattson, W.J.; Slocum, S.S.; Koller, C.N. 1983. Spruce budworm (*Choristoneura fumiferana*) performance in relation to foliar chemistry of its host plants. Pages 55-56 *in* Proc. Forest defoliator – host interactions: a comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-85.

McAndrews, J.H. 1967. Pollen analysis and vegetational history of the Itasca region, Minnesota. Pages 219-236 *in* E.J. Cushing and H.E. Wright, Jr., eds. Quarternary paleoecology. Yale Univ. Press, New Haven, Conn.

McKnight, M.E. 1968. A literature review of the spruce, western, and 2-year-cycle budworms. U.S. Dep. Agric., For. Serv., Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo. Res. Pap. RM-44.

McKnight, M.E. 1971. Natural mortality of the western spruce budworm, *Choristoneura occidentalis*, in Colorado. U.S. Dep. Agric., For. Serv., Rocky Mt. For. and Range Exp. Stn., Fort Collins, Colo. Res. Pap. RM-81.

Mehringer, P.J., Ferguson, C.W. 1969. Pluvial occurrence of bristle cone pine (*Pinus aristata*) in a Mohave desert mountain range. J. Ariz. Acad. Sci. 5:284-292.

Miller, C.A. 1963. The analysis of fecundity proportion in the unsprayed area. Pages 75-87 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Nichols, H. 1975. Palynological and paleoclimatic study of the late Quaternary displacement of the boreal forest-tundra ecotone in Keewatin and MacKenzie, N.W.T., Canada. Inst. Arct. Alp. Res., Univ. Colo., Boulder, Colo. Occas. Pap. 15.

Powell, G.R. 1977. Patterns of development in *Abies balsamea* crowns and effects of megastrobilus production on shoots and buds. Can. J. For. Res. 7:498-509.

Powell, J.A. 1980. Nomenclature of Nearctic conifer-feeding *Choristoneura* (Lepidoptera: Tortricidae): historical review and present status. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Gen. Tech. Rep. PNW-100.

Régnière, J.; Fletcher, R.M. 1983. Direct measurement of spruce budworm (Lepidoptera: Tortricidae) larval dispersal in forest stands. Environ. Entomol. 12:1532-1538.

Sanders, C.J. 1971a. Daily activity patterns and sex pheromone specificity as sexual isolating mechanisms in two species of *Choristoneura* (Lepidoptera: Tortricidae). Can. Entomol. 103:498-502.

Sanders, C.J. 1971b. Sex pheromone specificity and taxonomy of budworm moths. Science 171:911-913.

Sanders, C.J. 1975. Factors affecting adult emergence and mating behavior of the eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 107:967-977.

Sanders, C.J.; Daterman, G.E.; Ennis, T.J. 1977. Sex pheromone responses of *Choristoneura* spp. and their hybrids (Lepidoptera: Tortricidae). Can. Entomol. 109:1203-1220.

Sanders, C.J.; Lucuik, G.S. 1972. Factors affecting calling by female eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 104:1751-1762.

Sanders, C.J.; Weatherston, J. 1976. Sex pheromone of the eastern spruce budworm (Lepidoptera: Tortricidae): optimal blend of *trans*- and *cis*-11-tetradecenal. Can. Entomol. 108:1285-1290.

Shaw, G.G.; Little, C.H.A. 1977. Natural variation in balsam fir foliar components of dietary importance to spruce budworm. Can. J. For. Res. 7:47-53.

Shaw, G.G.; Little, C.H.A.; Durzan, D.J. 1978. Effect of fertilization of balsam fir trees on spruce budworm nutrition and development. Can. J. For. Res. 8:364-374.

Shepherd, R.F. 1985. A theory on the effects of diverse host-climatic environments in British Columbia on the dynamics of western spruce budworm. Pages 60-70 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept., 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Silen, R.R. 1973. First- and second-season effect on Douglas-fir cone initiation from a single shade period. Can. J. For. Res. 3:528-534.

Silen, R.R. 1978. Genetics of Douglas-fir. U.S. Dep. Agric., For. Serv., Washington, D.C. Res. Pap. WO-35.

Silen, R.R.; Mandel, N.L. 1983. Clinal genetic growth variation within two Douglas-fir breeding zones. J. For. 81:216-220.

Silk, P.J.; Wiesner, C.J.; Tan, S.H.; Ross, R.J.; Grant, G.G. 1982. Sex pheromone chemistry of the western spruce budworm *Choristoneura occidentalis* Free. J. Chem. Ecol. 8:351-362.

Sorensen, F.C. 1983. Geographic variation in seedling Douglas-fir (*Pseudotsuga menziesii*) from the western Siskiyou Mountains of Oregon. Ecology 64:696-702.

Stehr, G. 1964. The determination of sex and polymorphism in microevolution. Can. Entomol. 96:418-428.

Stehr, G. 1967a. On some concepts in the population biology of the spruce budworm. Proc. Entomol. Soc. Ont. 99:54-56.

Stehr, G. 1967b. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. II. Geographic distribution in accordance with forest regions. Can. Entomol. 99:456-463.

Steiner, K.C. 1979. Variation in bud-burst timing among populations of interior Douglas-fir. Silvae Genet. 28:76-79.

Stock, M.W.; Castrovillo, P.J. 1981. Genetic relationships among representative populations of five *Choristoneura* species: *C. occidentalis*, *C. retiniana*, *C. biennis*, *C. lambertiana*, and *C. fumiferana*. Can. Entomol. 113:857-865.

Terasmae, J. 1974. An evaluation of methods used for reconstruction of Quaternary environments. *In* W.C. Mahaney, ed. Quaternary environments: proceedings of a symposium, York Univ. Geogr. Monogr. 5:5-32.

Thomas, A.W. 1976. Effects of temperature on emergence of second-instar spruce budworm larvae. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-60.

Thomas, A.W. 1983. Foliage consumption by 6th-instar spruce budworm larvae, *Choristoneura fumiferana* (Clem.), feeding on balsam fir and white spruce. Pages 47-48 *in* Proc. Forest defoliator – host interactions: a comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Northeast. For. and Range Exp. Stn., Broomall, Pa. Gen. Tech. Rep. 85.

Thomas, A.W.; Borland, S.A.; Greenbank, D.O. 1980. Field fecundity of the spruce budworm (Lepidoptera: Tortricidae) as determined from regression relationships between egg complement, forewing length, and body weight. Can. J. Zool. 58:1609-1611.

Thomson, A.J.; Shepherd, R.F.; Harris, J.W.E.; Silversides, R.H. 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia. Can. Entomol. 116:375-381.

Tsukada, M. 1982. *Pseudotsuga menziesii* (Mirb.) Franco: its pollen dispersal and late Quaternary history in the Pacific Northwest. Jap. J. Ecol. 32:159-187.

Volney, W.J.A.; Liebhold, A.M.; Waters, W.E. 1984. Host associations, phenotypic variation, and mating compatibility of *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae) populations in south-central Oregon. Can. Entomol. 116:813-826.

Volney, W.J.A.; Waters, W.E.; Akers, R.P.; Liebhoid, A.M. 1983. Variation in spring emergence patterns among western *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in southern Oregon. Can. Entomol. 115:199-209.

von Rudloff, E. 1975. Volatile leaf oil analysis in chemosystematic studies of North American conifers. Biochem. Syst. Ecol. 2:131-167.

Wagg, J.B. 1958. Environmental factors affecting spruce budworm growth. Oreg. For. Lands Res. Cent., Corvallis, OR. Res. Bull. 11.

Wagner, M.R.; Blake, E.A. 1983. Western spruce budworm consumption — effects of host species and foliage chemistry. Pages 49-54 *in* Proc. Forest defoliator — host interactions: a comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Northeast. For. and Range Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-85.

Wellington, W.G. 1954. Atmospheric circulation processes and insect ecology. Can. Entomol. 86:313-333.

Wellington, W.G. 1980. Dispersal and population change. Pages 11-24 *in* A.A. Berryman and L. Safranyik, eds. Proc. 2nd IUFRO conf. on dispersal of forest insects. Washington State University, Pullman.

Willhite, E.A.; Stock, M.W. 1983. Genetic variation among western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae) outbreaks in Idaho and Montana. Can. Entomol. 113:41-54.

Wright, H.E., Jr. 1971. Late Quaternary vegetational history of North America. Pages 425-464 *in* K.K. Turekian, ed. The late Cenozoic glacial ages. Yale Univ. Press, New Haven, Conn.

Wright, J.W.; Kung, F.H.; Read, R.A.; Lemmien, W.A.; Bright, J.N. 1971. Genetic variation in Rocky Mountain Douglas-fir. Silvae Genet. 20:54-60.

Workshop I —

Population Dynamics

How close are we to predicting the occurrence, severity, and duration of budworm outbreaks?

Workshop I — Population Dynamics

Moderator: ***M.W. McFadden***

International Forestry, USDA Forest Service, Washington, D.C.

On behalf of the seven Discussion Leaders and their many panelists, I would like to welcome each of you to this workshop on population dynamics. In a sense, the workshop is a continuation of the synthesis papers that were presented this morning except that the format is that of a discussion group and only the Discussion Leaders are aware of the subjects that will be discussed.

The workshop actually consists of two parts. The first part will consist of six panels that will seek to illuminate us on the roles various biotic and abiotic factors in regulating numbers of budworms. The six panels will be discussing:

1. Environmental Factors
2. Predators
3. Parasites
4. Diseases
5. Budworm Behavior, and
6. Host-Plant Interactions

The second part will have only one discussion group and it will explore what we can learn from the historical records of budworm outbreaks and what are the theoretical interpretations that can be made from these records.

Before beginning, I would like you to know that I have asked each of the seven Discussion Leaders to present a brief overview of the research that has been carried out on that particular topic during the life of the CANUSA Program. I have also asked them to introduce each of the members of the panel and through their good leadership, to apprise us, in a timely manner, of the progress that has been made in understanding the influence of each of these regulating mechanisms on budworm population dynamics. The Discussion Leaders will focus their discussions on significant accomplishments and try to resolve issues or questions that might have been raised in the earlier session. Finally, I have asked the Discussion Leaders to try and leave time for you to pose questions to individual panel members or to the panel as a whole.

The workshop is scheduled to run from 3:00 until 6:30 PM tonight without a break. There is a wealth of information to be presented and so rather than impinge on an already tight schedule, I will ask Alan Thomson of the Pacific Forestry Research Centre at Victoria, British Columbia, to begin the first session.

Au nom des sept animateurs et des nombreux participants aux tables rondes, j'aimerais souhaiter à chacun de vous la bienvenue à cet atelier sur la dynamique des populations. Dans un sens, cet atelier donne suite aux communications de synthèse qui ont été présentées dans la matinée, sauf que la discussion se fera en groupes et que seuls les animateurs connaissent les sujets dont on traitera.

L'atelier se divise en deux parties. La première consistera en six tables rondes autour desquelles nous chercherons à nous éclairer sur les rôles des divers facteurs biotiques et abiotiques de régularisation des effectifs des tordeuses. Les six sujets de discussion seront:

1. Les facteurs du milieu
2. Les prédateurs
3. Les parasites
4. Les maladies
5. L'éthologie de la tordeuse
6. Les interactions entre les hôtes et les plantes.

Dans la seconde partie, il n'y aura qu'un groupe de discussion, qui explorera ce que nous pouvons tirer des antécédents des infestations et les interprétations théoriques possibles de ces antécédents.

Avant de commencer, j'aimerais vous annoncer que j'ai demandé à chacun des animateurs de faire un bref survol de la recherche réalisée grâce au programme CANUSA sur le sujet qui lui a été confié. Je lui ai aussi demandé de présenter chacun des membres de la table ronde et, en orientant les échanges, de nous informer, au moment opportun, de l'acquis des connaissances sur l'influence de chacun de ces mécanismes régulateurs. Les animateurs orienteront les discussions sur les réalisations notables et tenteront de répondre aux questions qui pourraient avoir été posées au cours de la séance antérieure. Enfin, j'ai demandé à chacun d'essayer de nous aménager du temps pour que vous puissiez poser des questions à un ou à tous les membres de la table ronde.

L'atelier devrait se tenir de 15 h à 18 h 30, sans interruption. La masse de renseignements à présenter est énorme et plutôt que d'empiéter sur un horaire déjà très chargé, je demanderai à M. Alan Thompson du Centre de recherches forestières du Pacifique, à Victoria, d'ouvrir la première séance.

Discussion Group A —
Environmental Factors

Temperature and Western Spruce Budworm Development

W.J. Kemp

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Host plant and insect pest phenology are generally considered to be critical elements in the modeling of defoliating insect population dynamics. Springtime synchrony between host trees and insect defoliators, such as the western spruce budworm (*Choristoneura occidentalis* Freeman), has proved to be an important contributor to outbreak development (Thomson el al. 1984).

Recent studies by Beckwith and Kemp (1984), Dennis et al. (1985),[1] Kemp and Beckwith (1985),[2] and Kemp et al. (1985)[3] have determined that it is possible to model western spruce budworm and host tree phenology as a function of accumulated degree days during a given year. The results of these studies further suggest that synchrony between the western spruce budworm and its host has an influence on subsequent defoliation levels. The methods and findings of the studies are outlined in this summary.

Data on western spruce budworm and host tree development were collected from two plots on the Starkey Experimental Forest near La Grande, Oregon. Details on the experimental design used for data collection before model building may be found in Beckwith and Kemp (1984), Kemp and Beckwith (1985)[2] for host tree species phenology, and Kemp et al. (1985)[3] for western spruce budworm phenology.

Concurrent with both larval and host development sampling, data on heat unit accumulation (degree days) above 5.5° C (42° F) were collected at each plot (two plots total) through the use of biophenometers. Biophenometers provided data on the accumulation of degree days from plot establishment (yearly) to each sample collection.

Data from Douglas-fir (*Pseudotsuga menziesii* Franco) and grand fir (*Abies grandis* (Dougl.) Lindl.) upper, mid, and lower crowns were used to develop host phenology models using a general logistic function (Beckwith and Kemp, 1984; Kemp and Beckwith, 1985[2]).

A detailed explanation of the model used to describe the phenology of the western spruce budworm may be found in Dennis et al. (1985)[1] and Kemp et al. (1985).[3] The model assumes that the proportion of the population in each development stage for a sampling date is calculated through the use of the logistic probability distribution.

Additional observations showed that defoliation of Douglas-fir on the Bear Springs plot in 1982 was light to moderate whereas in 1983 defoliation was much heavier. In an effort to examine whether there were differences in host and western spruce budworm phenology between the two years, the phenology models developed each year were compared. Figure 1 (a, b) shows a comparison of host and insect phenology models for the Bear Spring Plot in 1982 and 1983. Proportions on the ordinate of each graph indicate the proportion of the western spruce budworm population in instar II (I–2, Fig. 1) and instar III (I–3, Fig. 1) as a function of accumulated degree days. In the case of Douglas-fir (TRE, Fig. 1), ordinate values are the proportion of the total shoot elongation for a given year expressed as a function of degree days.

Figure 1 shows that there were large differences in host and western spruce budworm phenology in 1982 and 1983. In 1982 when defoliation was characterized as light to moderate, host shoot elongation at the peak of instar III was less than 2 percent. Conversely, in 1983 when subsequent defoliation was characterized as heavy, Douglas-fir shoots were 23 percent expanded at the peak instar III budworm stage. Although no data are available on the survival of instars II and III budworms by year, the model comparisons show that the synchrony of the host and insect was much more conducive to early larval survival in 1983 when compared to 1982. Results suggest that the increase in defoliation on the Bear Springs plot in 1983 was at least in part related to better larval success in finding feeding locations in the early spring (Kemp and Beckwith 1985[2]; Thomson et al. 1984).

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[1] Dennis, B.; Kemp, W.P.; Beckwith, R.C. 1985. A stochastic model of insect phenology. I. Estimation and testing. (in preparation).

[2] Kemp, W.P.; Beckwith, R.C. 1985. A comparison of phenology models developed for western spruce budworm host species in Northeastern Oregon and North Central Idaho. (in preparation).

[3] Kemp, W.P.; Dennis, B.; Beckwith, R.C. 1985. A stochastic model of insect phenology. II. The western spruce budworm. (in preparation).

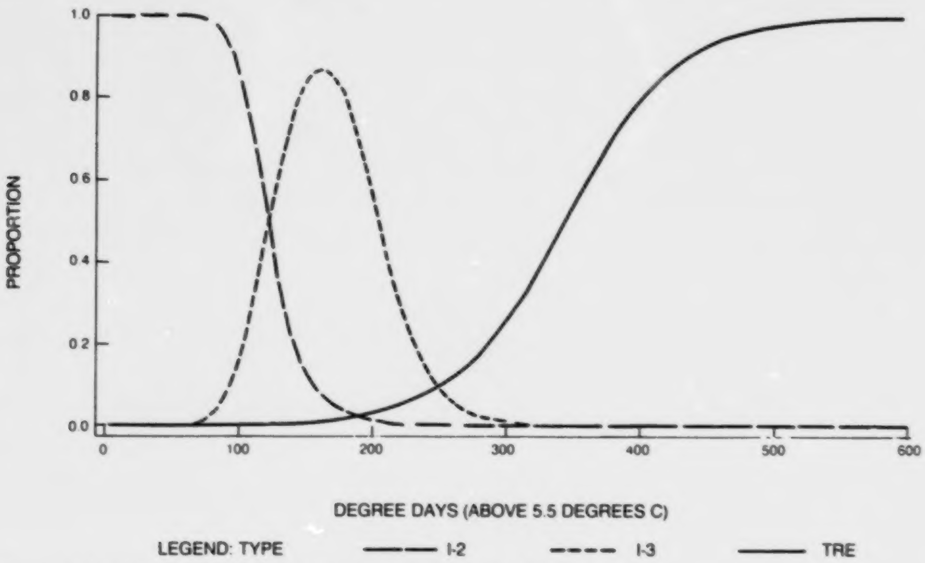

Figure 1. Comparison of Douglas-fir and western spruce budworm phenology models for larvae collected on Douglas-fir on the Starkey Experimental Forest, LaGrande, OR, 1982 (a) and 1983 (b).

Literature Cited

Beckwith, R.E.; Kemp, W.P. 1984. Shoot growth models for Douglas-fir and grand fir. For. Sci. 30(3):743-746.

Thomson, A.J., Shepherd, R.F., Harris, J.W.E., Silverside, R.H. 1984. Relating weather to outbreaks of western spruce budworm *Choristoneura occidentalis* (Lepidoptera: Tortricidae) in British Columbia. Can. Entomol. 116:375-381.

Discussion Group A —
Environmental Factors

Effects of Constant and Fluctuating Laboratory Temperature on the Western Spruce Budworm

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An insect's microclimate plays an important role in determining its survival and subsequent development. As an example, cool, wet weather during the larval stage of forest defoliators often delays development, thus exposing the insect to longer periods of natural controls. Laboratory studies are often conducted at constant temperatures; however, fluctuating temperatures are characteristic of an insect's environment. Therefore, caution must be used when attempting to apply development rates of insects reared at constant temperatures to natural field situations. A study was conducted in 1983 to determine the effect of a constant and a fluctuating temperature on the western spruce budworm (*Choristoneura occidentalis* Freeman).

Methods

Budworm larvae were reared in standard environmental control cabinets held at a constant 20°C (68°F) temperature or a fluctuating temperature around a 20°C (68°F) mean. The fluctuating temperature ranged from 10°C to 32°C (50°F to 90°F) during every 24-hour period. A constant 16/8 photoperiod was used throughout the experiment. Second instars were reared individually on standard artificial diet in small petri dishes until pupation. The pupae were weighed, sexed, and placed in clean dishes until adult emergence. Only those individuals that emerged as adults were used in the analysis.

Results

Survival to adults did not significantly differ at the two test temperatures. In both sexes, larval and pupal duration was significantly reduced when reared under fluctuating temperature as compared to the 20°C (68°F) constant temperature (Table 1). This reduction is similar to that found by researchers working with other insects (Messenger 1964; Hagstrum and Leach 1973). The fluctuating temperature also produced significantly heavier male pupae. The mean female pupal weight did not differ significantly between the test temperatures.

The results suggest that western spruce budworm development data obtained under constant temperatures cannot be directly applied to a field situation without considering some type of correction factor.

Table 1
Some effects of temperature on western spruce budworm under laboratory conditions

Sex	*Test temperature*	*No. of insects*	*Mean larval duration (days)*	*Standard deviation*	*Mean pupal duration (days)*	*Standard deviation*	*Mean pupal weight (mg)*	*Standard deviation*
Male	*20°C*	*35*	*33.3a**	*2.15*	*11.1a*	*0.49*	*116.3a*	*20.04*
	fluctuating	*27*	*25.4b*	*2.76*	*8.0b*	*0.59*	*129.4b*	*16.06*
Female	*20°C*	*28*	*35.7a*	*3.21*	*10.5a*	*0.64*	*185.5a*	*28.63*
	fluctuating	*30*	*26.6b*	*2.50*	*7.9b*	*0.57*	*204.8a*	*34.86*

*Any two means by sex not having a common letter are significantly different at the 0.05 probability level.

Literature Cited

Hagstrum, D.W.; Leach, C.E. 1973. Role of constant and fluctuating temperatures in determining development time and fecundity of three species of stored-products Coleoptera. Ann. Entomol. Soc. Am. 62:407-410.

Messenger, P.S. 1964. The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid, *Therioaphis maculata*. J. Econ. Entomol. 57:71-76.

Discussion Group A —
Environmental Factors

Effect of Weather on Spruce Budworm Populations

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There is evidence (Wellington 1952; Greenbank 1963) that spruce budworm outbreaks are preceded by a number of years in which there is a predominance of dry polar air during the larval feeding period, caused by a southerly shift in the tracks of low pressure systems across eastern North America. Our own work in Ontario (available as a file report) attempted to correlate the rise and fall of outbreaks in Ontario during the period 1930-1970 with the passage of low pressure systems by recording the numbers of cylcones and anticyclones (taken from the Monthly Weather Review) passing 20° N or 20° S of two reference points in Ontario during June and July each year. In addition we recorded mean temperature, mean monthly precipitation, mean daily temperature range, mean monthly sunshine and a summer weather index (Davis 1968), summarized from 43 weather stations in Ontario.

Fourteen distinct outbreaks occurred during the period. Twelve started after periods of wide daily temperature range, 12 after low precipitation, and 10 after a combination of the two. Declining outbreaks did not correlate with any of the parameters. The start of outbreaks in Ontario also appeared to be correlated with a northerly shift in the storm tracks and with a reduction in the total number of cyclones and anticyclones (i.e., more stable air) in June and July, all of which leads to warmer, drier air.

We concluded from this study that although the results confirm the theory that spruce budworm outbreaks are influenced by macrometeorological events, it is not possible to predict the time and location of the start of an outbreak from these parameters alone.

Table 1
Relationship between spruce budworm infestations and low temperature and high rainfall during and after emergence of second-instar larvae in Ontario, 1938-1978

Climatic condition	*Collapse of infestation %*	*No reduction in infestation %*
Number of events	*(38)*	*(328)*
Temp. below −6.0°C (21.2°F)	*24*	*3*
Rainfall above 35 mm (1.3 in)	*50*	*5*
Both of above	*2*	*0*
Neither of above	*24*	*92*

G.S. Lucuik

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In an attempt to explain how temperature and precipitation might affect population dynamics, we recently focused on their effects on the survival of second instar larvae in the spring. An analysis of precipitation and temperature showed that the collapse of the outbreaks was associated with high rainfall at the time of emergence and freezing temperatures following emergence (Table 1).

A laboratory experiment was carried out to investigate the role of rainfall in more detail. Balsam fir and white spruce branches were collected from an area of high budworm density in March 1979, set up in a greenhouse, and sprayed with a mist of water totalling 25 mm (1 in) per day to simulate rain. Each day, branches were removed from this regime and placed in darkened boxes from which the emerging larvae were collected. Table 2 shows that the numbers of insects emerging decreased with increasing "rainfall." Washing the branches with NaOH after the experiment showed that although the numbers of dead insects in hibernacula increased slightly, most were "missing," presumably washed off during emergence.

These data indicate that rainfall and low temperature have a profound effect on survival of small larvae, and that inclement weather during the period of larval emergence could cause large reductions in population density.

Table 2
Numbers of larvae emerging from hibernacula after various lengths of simulated rainfall

	Numbers of larvae/branch		
Days of "rain"	*Emerging from hibernacula*	*Dead in hibernacula*	*"missing"*
0	*13.3*	*2.9*	*0*
1	*11.5*	*2.5*	*2.2*
2	*11.0*	*2.9*	*2.4*
3	*6.8*	*3.4*	*6.0*
4	*5.4*	*4.8*	*6.0*
5	*3.2*	*5.2*	*7.8*
6	*3.0*	*5.0*	*8.2*
7	*3.3*	*5.8*	*7.1*
8	*2.3*	*5.5*	*9.4*

Literature Cited

Davis, N.E. 1968. An optimum summer weather index. Weather 23:305-317.

Greenbank, D.O. 1963. The development of the outbreak. *In* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entmol. Soc. Can. No. 31. 332 p.

Wellington, W.G. 1952. Air mass climatology of Ontario north of Lake Huron and Lake Superior before outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Tortricidae; Lasiocampidae). Can. J. Zool. 30:114-127.

Discussion Group A —
Environmental Factors

The Role of Environmental Factors in the Population Dynamics of Western Spruce Budworm in British Columbia

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At the Pacific Forest Research Centre we have studied the effects of temperature and elevation on rate of development of *C. occidentalis* larvae and timing of budflush of Douglas-fir. We have also studied wind patterns in mountainous terrain, as they relate to moth flight.

Heat unit requirements for budflush had a temperature threshold, total heat unit requirement, and starting date for accumulation, different from those published for budworm larvae (Thomson and Moncrieff 1982). As a result, annual variability in weather patterns caused variability in timing of larval emergence and budflush (Thomson et al. 1984a).

Changes in temperature with elevation were studied using an empirical approach, which allowed for the effects of solar heating of the foliage (Thomson et al. 1983). The study of budflush also allowed for solar heating effects.

Solar heating has been studied more explicitly through the use of digital terrain models which permit evaluation of topographic shading, and the relationship of heat input to slope and aspect (Thomson and Moncrieff 1979; Thomson et al. 1984b).

Wind patterns were observed in the field through the use of meteorological recording stations and by following released balloons. An image-intensifying, night-viewing scope was used to observe moth flight which occurred around the time of changeover from afternoon up-slope winds to nocturnal downslope drainage winds; i.e., when the air was relatively still. Wind patterns at the time of larval or moth dispersal are also being studied through the use of digital terrain models in conjunction with numerical wind models (Thomson et al. 1984b).

All these environmental effects are considered in a simulation model of western spruce budworm population dynamics (Thomson 1979).

Literature Cited

Thomson, A.J. 1979. Evaluation of key biological relationships of the western budworm and its host trees. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Info. Rep. BC-X-186. 19 p.

Thomson, A.J.; Moncrieff, S.M. 1979. Computer graphics display of topographic data. Can. For. Serv., Ottawa. Bi-mon. Res. Notes 35(1):4-5.

Thomson, A.J.; Moncrieff, S.M. 1982. Prediction of bud burst in Douglas-fir by degree day accumulation. Can. J. For. Res. 12:443-452.

Thomson, A.J.; Harris, J.W.E.; Silversides, R.H.; Shepherd, R.F. 1983. Effects of elevation on the rate of development of western spruce budworm (Lepidoptera: Tortricidae), in British Columbia. Can. Entomol. 115:1181-1187.

Thomson, A.J.; Shepherd, R.F.; Harris, J.W.E.; Silversides, R.H. 1984a. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia. Can. Entomol. 116:375-381.

Thomson, A.J.; Moncrieff, S.M.; Silversides, R.H. 1984b. Use of digital terrain models in studies of western spruce budworm population dynamics and impact. CANUSA Newsletter. No. 34, May 1984.

Discussion Group A —
Environmental Factors

Temperature Effects on Development and Survival of Western Spruce Budworms

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Individual western spruce budworm developmental times have a skewed, unimodal distribution for which the log-normal distribution is an adequate model. Developmental time variances are often greater within than among families (Volney et al. 1983), particularly for early instar development (Volney et al. 1984a).[1] This pattern guarantees that representatives of most families will survive whatever the degree of synchrony between the insect and host development. Synchrony between insect emergence and phenological windows in which feeding sites are established may be a major determinant of early instar survival, however. Any process, such as flowering, which effectively increases this window's size can further influence survival rates.

As temperature increases, insect developmental rates (DR) are accelerated nonlinearly at low, almost linearly in intermediate, and retarded at high temperatures; but with increases beyond the maximum DR temperature, retardation is rapid as upper lethal temperatures are approached. For western spruce budworms, temperatures at which these rate changes occur increase with the insect's physiological age (Volney et al. 1984a).[1] This pattern allows budworms to track their thermal environment which becomes warmer as they age.

Some developmental rate variation among populations in the early instars is attributable to differences between the sibling species *Choristoneura occidentalis* Freeman and *C. retiniana* (Walsingham). Early development of each species appears closely tuned to that of its principal host until they enter the sixth instar. True firs, the principal hosts of *C. retiniana*, flush first but their shoots develop slower than those of Douglas-fir, the principal host of *C. occidentalis* (Volney et al. 1984b). Coincidentally, although *C. retiniana* emerges first, its development in the early instars is slower than that of *C. occidentalis* larvae (Volney et al. 1984a).[1] Life table analyses (Volney and Waters, unpublished) indicate that high early instar survival is correlated with high population trends.

Temperature influences sixth instar, pupal, and adult coloration. Pigmented areas of insects reared at high temperatures tend to be lighter than their counterparts reared at low temperatures (Volney et al. 1983b). Males tend to be darker than females and hybrid individuals are more labile in their color response than either parental morph. These temperature reactions may function in thermal regulation because radiation is an important source of thermal energy in the insects' natural environments. Further, morphological plasticity would tend to stabilize insect development across forest stands with different thermal environments. Beyond the fifth instar, there are no developmental differences between species. However, brown larval morphs of hybrid families spend longer as sixth instars than their less pigmented sibs. Thermal regulation may also stabilize development of hybrids in nature.

Although temperature has a profound effect on daily male trap catch, the onset of male response to pheromone sources is earlier on cool than on warm evenings (Liebhold and Volney 1984). Thus, mating is possible on evenings when temperatures fall below male flight thresholds at sunset.

In both species there is some value in a protracted Spring emergence but synchronized adult development becomes paramount for mating. Variation in total development time may be reduced by selection of individuals emerging in the phenological window which allows feeding site establishment. But budbreak is an unpredictable event and selection in any one season would render the population maladapted for subsequent seasons. Significant negative correlations between development times at different life stages is one way in which early developmental variation be can conserved while reducing variation in moth eclosion dates (Volney et al. 1984a).[1] The similarity in developmental controls of the two budworm species studied suggest that similar mechanisms may operate in other *Choristoneura* spp.

Literature Cited

Liebhold, A.M.; Volney, W.J.A. 1984. Effects of temporal factors on reproductive isolation between *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae). Can. Entomol. 116:991-1005.

Volney, W.J.A.; Waters, W.E.; Akers, R.P.; Liebhold, A.M. 1983a. Variations in spring emergence patterns among western *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in southern Oregon. Can. Entomol. 115:199-209.

---

[1] Volney, W.J.A.; Liebhold, A.M. 1984a. Post diapause development of sympatric *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae) populations and their hybrids (In preparation).

Volney, W.J.A.; Liebhold, A.M.; Waters, W.E. 1983b. Effects of temperature, sex, and genetic background on coloration of *Choristoneura* spp. (Lepidoptera: Tortricidae) populations in south-central Oregon. Can. Entomol. 115:1583-1596.

Volney, W.J.A.; Liebhold, A.M.; Waters, W.E. 1984b. Host associations, phenotypic variation, and mating compatibility of *Choristoneura occidentalis* and *C. retiniana* (Lepidoptera: Tortricidae) populations in south-central Oregon. Can. Entomol. 116:813-826.

Discussion Group A — Environmental Factors

Summary

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Environment may be defined as the sum total of all external influences acting on an organism or on part of an organism. The present discussion, however, is restricted to direct effects of weather, and can be divided into three main subject areas:

1. effects of temperature on rates of development
2. relative timing of events: phenology
3. effects of extremes of weather on survival

This summary addresses these three main areas, not only the material submitted by the discussion group members, but also material presented in the invitational papers of the symposium.

Larval emergence and development to particular stages is associated with accumulation of a fixed number of heat units in many studies. Similarly, host bud and shoot development have been related to heat unit accumulation. In general, this concept is useful, but some studies have demonstrated that the heat unit total required for a particular stage may vary from year to year and place to place. For example, degree of fluctuation of the temperature regime affects developmental rate, and different color morphs have different rates. Also, heat unit totals are evaluated from air temperatures, whereas the temperature within needles, buds, and larval hibernacula can be greatly increased by direct solar insolation.

As budworm larvae and buds of different host species have different temperature thresholds, starting dates for accumulation and required heat unit totals, the synchronization of larval emergence, and budflush can vary widely from year to year and location to location. An optimal degree of synchronization allows larvae to penetrate swollen buds. As little as a week's asynchronization can mean that larvae cannot penetrate buds or become exposed to direct adverse effects of weather, or face a very different host foliar chemistry. Host flowering, which may be related to drought stress, can modify effects of vegetative bud phenology. Phenological effects have been related to onset and collapse of western spruce budworm populations. Flowering has been related to increase of eastern populations.

Because the timing of different stages varies from year to year, weather at a specific time of year does not always act on the same stage of development. In addition, in mountainous terrain, rates of development decrease with increased elevation so that an event such as a storm acts on a range of developmental stages. It is, therefore, essential to relate weather effects to specific stages of development rather than time of year, as effects may vary with stage. For example, warm weather may enhance large larval survival and adult mating and oviposition but have an adverse effect on the eggs and larvae in their hibernacula.

High rainfall at the time of larval emergence, or freezing temperatures following emergence, are associated with outbreak collapses. Warm dry summers, especially following an optimal synchronization of budflush and larval emergence, are associated with the onset of outbreaks. Periods of prolonged high temperatures following oviposition are associated with outbreak collapse in British Columbia.

As weather events have been related to both outbreak origin and collapse, some researchers believe that the expected frequency and duration of outbreaks in a region can be estimated from the long-term weather record. This may be especially true in the west where endemic population levels appear to be higher than in the east, resulting in possible release of the population by weather events acting in a single year.

Discussion Group A —
Predators

Effects of Bird Exclusion on Budworm Populations in Northwestern Ontario

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Density dependent mortality of spruce budworm at low densities is an essential component of the UBC/CFS computer-simulation model (Jones 1977), and it has been proposed that birds are the agent responsible.

Because of the importance of this assumption to the behavior of the model, we decided to exclude birds from a susceptible area of forest to see if the budworm population would increase to outbreak levels. A joint investigation was sponsored by the Canadian Forestry Service, Canadian Wildlife Service, and Queen's University, near Black Sturgeon Lake, northwestern Ontario, where budworm populations were low.

We attempted to remove the birds from a 10-ha (25-acre) plot; 57 birds were shot in 6 weeks, but of 21½ territories occupied by singing males at the start, 7½ were still occupied at the end. Difficulty in locating the birds suggested that shooting them all was impractical, and cages to exclude birds were built instead.

Two cages were built in the spring of 1980, 17-m (55-ft) square in cross section and about 16-m (50-ft) high. Television antennae towers were used as corner posts, guyed by steel wire rope, which was also strung between the posts to support Conwed black plastic "bird-damage-control netting," 1.5 × 1.35 strands/inch. Parasites, spiders, and other arthropods could pass through the mesh but not birds. Budworm moths could pass through the screen easily, although it may have hindered their flight.

Each year starting in 1980, the screen was put up in May and removed in August. Temperatures inside and out differed by less than 0.5°C, and relative humidity by 5 percent. Because removal of the branches would effect the results, budworm populations were estimated from the ground by the use of binoculars. Buds with visible evidence of spruce budworm larvae were recorded, and expressed as a percentage of the total number of buds inspected. Estimates were carried out during the sixth instar, when evidence of larvae is obvious.

In the second year, density of budworm was higher inside the cages (Table 1). But in 1983 and 1984, when the budworm populations increased dramatically near Black Sturgeon Lake, differences were no longer significant. Effects of bird predation detectable in 1981 were probably masked by invasion of moths and dispersing larvae into the Black Sturgeon Lake area in 1982: that moth dispersal was seen for the first time in the area in 1982 may be significant.

Table 1
Population densities of sixth instar spruce budworm inside and outside bird exclosures, Black Sturgeon Lake, northwestern Ontario

	Balsam fir shoots infested by budworms			
	Caged populations		*Uncaged populations*	
Year	*A*	*B*	*A*	*B*
		Percent		
1980	*0.68*	*0.85*	*0.54*	*0.77*
1981	*2.27*	*2.34*	*0.50*	*0.58*
1982	*9.0*	*17.6*	*10.1*	*13.9*
1983	*22.4*	—	*16.1*	—

Our results are inconclusive. Although we are still interested in the effects of bird predation on low populations of budworm in Ontario, current high-density populations make further studies difficult.

Literature Cited

Jones, D.D. 1977. The budworm site model. *In* G.A. Norton and C.S. Holling, eds. Proc. conference on pest management, 25-29 Oct. 1976. Int. Inst. for Appl. Syst. Anal., A2361, Laxenburg, Austria. 352 p.

Discussion Group A —
Predators

Some Effects of the Chemical Suppression of Western Spruce Budworm on Predaceous Forest Ants

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Recent studies (Campbell and Torgersen 1982; Campbell et al. 1983) have shown the importance of predaceous ants in the dynamics of western spruce budworm populations in the Northwest. Predaceous ants have their greatest effect on the budworm during the late larval and pupal stages when budworm density is low. These findings encourage future research on the use of forest ants as biological components in an integrated budworm-management program. Current management centers on the suppression of outbreak populations by application of insecticide. This tactic is potentially damaging to forest ant populations.

In 1983, during a budworm suppression project in Oregon, I examined possible effects of aerial applications of carbaryl on the foraging activity of predaceous forest ants. I examined foraging levels in two places within treated areas and at two untreated sites. Data analyses are not yet complete; however, preliminary chi-square analysis indicates ant foraging activity was significantly reduced ($P < 0.001$) on the postspray treated sites compared with the control areas. Foraging activity remained at lower than pretreatment levels for the duration of the sampling period, which ended 6 weeks after the spray.

Whether the reduction in foraging resulted from direct mortality of foraging workers, ingestion of poisoned prey items by colony members, or for other reasons is not clear. Activity in at least one colony completely stopped after the spray. Another colony at the same site remained active even though foraging activity surrounding it was sharply reduced.

Reducing oubreak populations by spraying may also inhibit a significant portion of the natural enemy complex, which could help keep those populations sparse. Conceivably, reducing the natural enemies may contribute to resurgence of budworm populations in some areas.

If the use of natural enemies is to become part of a budworm-management program, more research is needed to evaluate the response of the natural enemy complex to various control tactics. To make informed decisions, managers must be aware of the extent to which control methods may be incompatible.

The data indicate that suppression of budworm populations with carbaryl adversely affects the foraging of predaceous ants during at least that budworm generation. I can only speculate on the extent of ant mortality, the ability of ant colonies to rebound to former foraging levels, or on what this may mean in terms of future management approaches.

Literature Cited

Campbell, R.W.; Torgersen, T.R. 1982. Some effects of predaceous ants on western spruce budworm pupae in north-central Washington. Environ. Entomol. 11:111-114.

Campbell, R.W.; Torgersen, T.R.; Srivastava, N. 1983. A suggested role for predaceous birds and ants in the populations dynamics of the western spruce budworm. For. Sci. 29:779-790.

Discussion Group A —
Predators

Ant Predators of the Western Spruce Budworm: Species Composition and Patterns of Occurrence in Eastern Oregon and Western Montana

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Predation by insectivorous birds and foliage-foraging ants is significant in the population dynamics of the western spruce budworm. These two groups of predators are the source of most of the mortality of budworm during the late larval and early pupal period, and may be the principal factor responsible for maintaining budworm populations at sparse densities (Campbell, in press).

The identity and distribution of ant species preying on the western spruce budworm was investigated in eastern Oregon and western Montana. A sticky trap was developed to index ant-foraging activity in the canopy by intercepting ants falling as they traveled between the canopy and the ground. For all common ant species, trap catches were highly correlated with the average number of ants moving up the bole. Thus, traps indexed both species composition and density of ants foraging in the canopy.

Ant species preying on pupae of the budworm were investigated on two sites in eastern Oregon in 1981, and four sites in eastern Oregon and six sites in western Montana in 1982. Predation was observed by hourly examination of stocked pupae on trees actively foraged by ants.

The following ant species and numbers were collected as they fed on budworm pupae: *Camponotus modoc* Wheeler, 160; *C. laevigatus* (Smith), 53; *C. vicinus* Mayr, 48; *Formica obscuripes* Forel, 174; *F. podzolica* Francoeur, 43; *F. accreta* Francoeur, 32; *F. neorufibarbis* Emery, 12; *F. lasioides* Emery, 1; *F.* sp. (*microgyna* group), 1. The *Camponotus* species and *F. obscuripes* comprised 85 percent of all ants preying on budworm pupae. Additional species of *Formica* and *Camponotus* have been observed or implicated as budworm predators: *F. haemorrhoidalis* in north-central Washington (Campbell and Torgersen 1982); *F. criniventris* in western Montana (Bain 1974); and *F. subnuda*, *F. argentea*, and *C. herculeanus* in Idaho.[1]

The distribution of canopy-foraging ant species was studied on 24 sites in Montana and 24 sites in Oregon. Sites were selected along a moisture-temperature gradient indexed by vegetational composition (habitat type). Ants were sampled using sticky traps, and several site and stand variables were correlated with an abundance of ants collected at each site.

Nine species of *Formica* and *Camponotus* were collected in Montana and 11 species in Oregon. Four species were common in both states — *C. modoc*, *C. vicinus*, *F. neorufibarbis*, and *F. podzolica*. In addition, *C. herculeanus* (L.) was common in Montana and *F. accreta* was common in Oregon. The distribution of these species varied among habitat types and between states, and the abundance of each was correlated with a different set of environmental variables. At least one ant species predaceous on the western spruce budworm was common in each habitat type in either state. Across almost all habitat types, each common species was more abundant in stands where average canopy coverage was less than 90 percent. The distribution of ant foragers in the canopy on each plot was highly aggregated in all species in both states.

Literature Cited

Bain, O.G. 1974. Two wood ant species attacking western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae) in western Montana. M.S. thesis. School of Forestry, University of Montana, Missoula, Mont.

Campbell, R.W. (In press). Population dynamics. Chapter 6 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech coords. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1694.

Campbell, R.W.; Torgersen, T.R. 1982. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. Environ. Entomol. 11:111-114.

---

[1] Markin, G.P. 1979. Ants as predators of the western spruce budworm. Paper presented at 1979 Entomol. Soc. Am. annual meeting, Denver, CO.

Discussion Group A — Predators

Role of Birds and Ants in Western Spruce Budworm Dynamics

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In 1979, R.W. Campbell and I attacked the extensive literature on natural enemies of spruce budworm and the more modest literature alluding to western spruce budworm enemies. References to avian predation held our particular interest and offered compelling arguments for pursuing studies on the activity of birds as budworm predators.

Combining our experience with natural enemies of gypsy moth (*Lymantria dispar* (L.)) and Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)), we decided that an exclusion method would be appropriate for examining avian predation processes. We also assumed that if such predation did influence budworm dynamics, it would do so at low, innocuous densities.

Initial studies using 0.8 m^3 (26 ft^3) single-branch exclosures (cages) were conducted in north-central Washington in 1979 (Torgersen and Campbell 1982). These exclosures were carefully placed over branches with naturally occurring budworm larvae. After pupation, the density of surviving pupae was determined. In some sites, survival to pupae was 2 or 3 times as high on caged branches as on controls. Not surprisingly, avian predation was stratified — greater mortalities occurred on trial branches at 5 m (16 ft) above the ground than at 2 m (6 ft). Because of differences in densities of budworms and of birds among sites, and of possible effects from other sources of mortality, conclusions concerning a regulatory role of birds had to await further studies. Concurrent studies by E.O. Garton (University of Idaho, Moscow) at the same Washington sites determined that at least five species of birds were actively feeding on budworm.

To determine predation during the pupal stage, twigs with naturally occurring pupae were wired to exposed or caged trial branches. At the conclusion of the first trial, we found that disappearance of pupae was high on both caged branches and control branches. The riddle was answered by the presence of several colonies of formicine ants in the study area. Subsequent supplementary trials were conducted with the use of sticky barriers at the base of sample branches to prevent access by foliage-foraging ants. Trials using branches with or without sticky barriers showed 85-percent pupal survival on treated branches compared to 8-percent survival on controls.

Additional trials using cage exclosures, sticky barriers, or both yielded a design that examined survival in the absence of birds, ants, or both, or no exclusion. These treatments were replicated at 2 and 5 m (6 and 16 ft). Pupal survival was much greater on all combinations of exclosure-treated branches than on controls. Specific effects of either birds or ants alone were difficult to interpret, however, because some ants gained access to some "protected" branches — mostly by dropping onto them from higher in the crown. Results clearly indicated, however, that birds and ants, alone or in concert, could have a profound effect on budworm survival (Campbell and Torgersen 1982).

The foregoing trials indicated further study of predator effects could add to our knowledge of budworm dynamics. Instead of using single-branch exclosures, we developed 9-m (30-ft) tall whole-tree exclosures (Campbell et al. 1981). Using combinations of these exclosures, sticky barriers, or both around the boles, we selectively excluded birds, ants, both, or neither from entire Douglas-fir or grand fir trees. We conducted whole-tree trials in Washington, Idaho, Oregon, and Montana in 1980 and 1981. Four trees were represented in each of 32 replications overall in the four geographical areas. Initial densities in 12 study sites were about 1.5 to 48 fourth instars per m^2 (10 ft^2). Trials with exclosures were set up after spring dispersal of larvae and before budflush. When seasonal budworm development was complete and adults had emerged, trial trees were dissected and exuviae or other pupal remains were removed and counted on 20 to 25 percent of the branches on each tree. Crown position of the sampled branches were tallied so that survival rates could be reconstructed by crown level. Thus, our survival data represent dissections of 128 nominal 9-m (30-ft) tall trees.

From these whole-tree trials, we determined that birds and ants alone or together had significant effects on budworm survival. Budworm survival from fourth instar to adult ($S_{L\text{-}A}$) on trees protected from birds and ants was consistently high across a range in host density (N_L) from about 2 to 31 L_{IV} per m^2 (10 ft^2). At these densities $S_{L\text{-}A}$ was about 30 to 90 percent. On control trees — those accessible to birds, ants, and other natural enemies — $S_{L\text{-}A}$ ranged from 5 percent at the lowest initial host densities, to 80 percent at the highest densities. Natural enemies caused about a 10-fold reduction in $S_{L\text{-}A}$ when N_L was low — about 2 L_{IV} per m^2 (10 ft^2). At the highest densities, >30 L_{IV} per m^2 (10 ft^2), natural enemies had virtually no effect on survival. Ants alone caused about a 5-fold reduction in survival at low host densities. Birds alone permitted survival to adults of only about 8 percent of the budworms on trees with low initial densities. This constituted about a 6-fold reduction in survival caused by birds alone. Little or no effect of either birds or ants alone was discernible on trees with high initial densities of budworm.

Effects of birds and ants on adult density, as measured by numbers of exuviae in relation to initial pupal density among treatments, were striking. On control trees these two predator guilds reduced adult density 10 to 15-fold among trials in low-density populations. Even when initial L_{IV} density was about 25 per m^2 (10 ft^2), adult density was about twice as high on trees where the budworm was protected from birds and ants as on unprotected control trees. (Campbell et al. 1983). Birds or ants consistently compensated for the absence of the other guild in these selective exclosure trials. Significantly, other mortality factors did not compensate for the absence of birds and ants where these guilds were both excluded (Campbell and Torgersen 1983). These data suggest a major role for insectivorous birds and foliage-foraging ants in the population dynamics of western budworm.

Literature Cited

Campbell, R.W.; Torgersen, T.R. 1982. Some effects of predaceous ants on western spruce budworm pupae in north-central Washington. Environ. Entomol. 11:111-114.

Campbell, R.W.; Torgersen, T.R. 1983. Compensatory mortality in defoliator population dynamics. Environ. Entomol. 12:630-632.

Campbell, R.W.; Torgersen, T.R.; Forrest, S.C.; Youngs, L.C. 1981. Bird exclosures for branches and whole trees. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, Oreg. Gen. Tech. Rep. PNW-125. 10 p.

Campbell, R.W.; Torgersen, T.R.; Srivastava, N. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. For. Sci. 29:779-790.

Torgersen, T.R.; Campbell, R.W. 1982. Some effects of avian predators on the western spruce budworm in north-central Washington. Environ. Entomol. 11:429-431.

Discussion Group A — Predators

Effects of Bird Predation on Spruce Budworm: A Pilot Study

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An advancing spruce budworm infestation in 1976 provided an opportunity to determine the species of birds that preyed on sparse, transitional, and outbreak populations of the spruce budworm.

Spruce-fir stands in central Maine and northern New Hampshire were selected to represent a range in insect densities. Bird populations were censused, and budworm densities were estimated using pheromone traps. Mid and upper crown defoliation were sampled on each plot, and branch surface areas were estimated.

Defoliation ranged from none to moderate. Defoliation per branch was positively correlated with number of moths per trap.

Breeding-bird populations differed among the stands, and their densities were positively correlated with moths per trap. In stands sparsely populated with budworm, the Nashville and Blackburnian warblers, golden-crowned kinglet, black-capped chickadee, and white-throated sparrow ate the most budworms. In stands with transitional budworm populations, red-winged blackbirds, white-throated sparrows, black-capped chickadees, and black-throated green and Cape May warblers consumed the most budworm larvae and pupae. In outbreak stands, all birds we sampled had eaten budworms. The mean number of budworms per bird stomach differed significantly between sparsely populated stands and stands with transitional or outbreak budworm populations.

We estimated that seasonal consumption by birds totaled over 3 300 larvae and 2 300 pupae per ha (1,335 and 931 per acre) in sparsely populated stands; 32 000 larvae and 22 000 pupae per ha (12,950 and 8,903 per acre) in transitional stands; and over 52 000 larvae and 36 000 pupae per ha (21,044 and 14,570 per acre) in outbreak stands. These figures conservatively approximate 87, 23, and 2 percent of the numbers of sixth instars, respectively.

Twelve of the 15 bird species we studied in detail ate more larvae and pupae as budworm numbers increased from sparse to transitional populations. Although our sample sizes were statistically inadequate to test within-species changes, we hypothesize that consumption by black-capped chickadees, red-breasted nuthatches, Blackburnian warblers, and white-throated sparrows increases substantially as budworm numbers begin to increase in outbreaks. Bird species that maintain high densities, high feeding rates, and respond to initial rises in insect numbers have the potential to maintain insect populations at low densities.

Bird populations may be increased by directed forest practices (Crawford and Titterington 1979; Titterington et al. 1979). The bird species we found important in sparsely populated stands require mature forests with tall conifer or brushy openings and with considerable edge or immature open conifers. Thus, a mature managed forest containing a mix of tree species and size classes with scattered openings and patches of regeneration should support populations of birds that prey effectively on spruce budworm.

More details of this study may be found in Crawford et al. (1983).

Literature Cited

Crawford, H.S.; Titterington, R.W. 1979. Effects of silvicultural practices on bird communities in upland spruce-fir stands. Pages 110-119 *in* R.M. DeGraaf and K.E. Evans, compilers. Management of North Central and Northeastern forests for non-game birds. U.S. Dep. Agric., North Central For. Exp. Stn. Gen. Tech. Rep. NC-51.

Crawford, H.S.; Titterington, R.W.; Jennings, D.T. 1983. Bird predation and spruce budworm populations. J. For. 81:433-435.

Titterington, R.W.; Crawford, H.S.; Burgason, B.N. 1979. Songbird response to commercial clearcutting in Maine spruce-fir forests. J. Wildl. Manage. 43:602-609.

Discussion Group A — Predators

Enhancing Habitat of Avian Predators

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Forest birds consume such large numbers of western spruce budworm that budworm populations increase dramatically on trees protected from birds. The economic value of this form of biological control exceeded $4700 per square mile per year on two Douglas-fir stands in north-central Washington. Simple economic analyses indicate that biological control of western spruce budworm by increasing bird populations may sometimes be cost effective. Bird populations change in response to changes in the tree, shrub, and ground-layer components of forest stands and in response to weather, changing insect densities, and availability of nest sites, water, and food resources. The shrub layer appears to be particularly important to many of the birds that feed on budworm. Stands in early successional stages, having very diverse and abundant bird communities, appear to be highly resistant to outbreaks of budworm. In later successional stages, potential avian predators are less abundant in more densely stocked, even-aged stands lacking a shrub understory. Silvicultural manipulation of such stands to increase shrub abundance and decrease stocking density would increase the effectiveness of avian predators of western budworm. Maintaining diverse forests of vigorously growing, less susceptible host species will be most successful where careful thought is given to maintaining avian predators and other natural enemies of western spruce budworm.

Discussion Group A — Predators

Effects of Birds and Ants on Pupae of the Spruce Budworm

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In 1982, stands supporting sparse populations of the spruce budworm were selected in northern New York, Vermont, and New Hampshire. Single branch enclosures and sticky barriers were used to exclude birds, ants, and both groups from budworm pupae placed on host trees. No effect of ants could be demonstrated; the effects of birds, while discernible, were minor.

In 1983, further trials on sparse budworm populations were conducted in northern New York. Whole-tree exclosures and sticky barriers were used to protect the budworm on trees about 4.5 m (15 ft) tall. After moth flight, we determined that either birds alone or ants alone had sometimes removed most of the planted pupae. On other plots, however, neither birds nor ants had any discernible effect.

The results for insectivorous birds tend to confirm what many prior investigators have already described, but results for foliage-foraging ants suggest that they may sometimes play a hitherto unsuspected role in the populations dynamics of the spruce budworm, at least in fringe-type habitats, such as those found in northern New York.

Discussion Group A — Predators

Preliminary Studies of the Relation between Spruce Budworm and Birds in the Boreal Forest of Ontario

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Although populations of some bird species dramatically increase in density during outbreaks of spruce budworm (Kendeigh 1947; Morris et al. 1958), the exact circumstances under which response occurs are not well understood. Selective cutting of mixed forests in northern Ontario has resulted in large areas of uneven-aged stands of mixed species, which provide large foliage volume for budworm. In mature forest stands, a large numeric response to high budworm density usually occurs by one or more of the budworm specialists (classically the Cape May, bay-breasted Tennessee, and Blackburnian warblers), with almost no change in density in other species. In the selectively cut stands near Manitouwadge, Ontario, we found that the response was faster and greater than usual and by species not usually thought to be budworm predators. On one plot, eight species of birds doubled their density in a 4-year period, during which overall avian density increased four-fold from 270 pairs/km^2 (0.038 mi.^{2}) to 1450 pairs/km^2 (0.038 mi.^{2}).

The effect of avian predation on the population dynamics of the budworm is even less well understood than the effect of budworm on birds. Following inconclusive studies with large exclosures (15 x 15 m, 50 x 50 ft) in 40-year-old, mixed-wood stands near Black Sturgeon Lake (Wypkema 1982), we conducted an intensive observational study in the same general area from mid-May to mid-July 1983, to attempt to quantify avian feeding rates on spruce budworm. During more than 250 hours of observing from scaffolds, we recorded over 1000 instances of birds foraging for budworm. Of 24 species that could conceivably feed on budworm, 18 were observed to do so.

Birds actively searched for and fed on budworm from the time the second instar emerged until pupation. Late in the season, birds fed on slowly developing larvae much more frequently than on pupae. Unexpectedly high budworm density (50/m^2 [10 ft^2] of foliage) made searching for prey almost unnecessary by fifth and sixth instars, at the peak of food demand by nestlings.

The superabundance of food coupled with the cryptic behavior of arboreal warblers when feeding young resulted in poor success in making foraging observations during the late stages of budworm development. Preliminary estimates of feeding rates have been established.

Literature Cited

Kendeigh, S.C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ontario Department of Lands and Forests. Biol. Bull. 1:1-100.

Morris, R.F.; Cheshire, W.F.; Miller, C.A.; Mott, D.G. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology 39:298-494.

Wypkema, R.C.P. 1982. The role of avian predators in the control of spruce budworm at endemic levels. Ph.D. thesis. Queens University, Kingston, Ontario.

Discussion Group A —
Predators

Summary

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Most of our panelists reported on the results of studies that were designed to clarify the role of predation in the population dynamics of either the spruce budworm or the western spruce budworm. Three investigators (Sanders [Ontario, Canada], Torgersen [northwestern states, U.S.A.], and Campbell [northeastern states, U.S.A.]) focused on the results of studies that featured predator exclusion. Others reported on results that were based primarily on either direct sampling and examination of predaceous birds (Crawford and Jennings [Maine and New Hampshire, U.S.A.]) or on repeated field observations on either predaceous ants (Youngs [Oregon and Montana, U.S.A.]), or birds (Welsh [Ontario, Canada]). Collectively, the results of these studies leave no doubt that predators play an important role in budworm population dynamics, particularly when the budworm populations are sparse.

Murphy reported on responses by predaceous forest ants to chemical suppression of the western spruce budworm. His preliminary analysis indicates that ant foraging in the year of treatment was significantly reduced on the treated sites.

Several investigators discussed the habitat requirements of predators. Youngs concentrated on the species composition and patterns of occurrence of predaceous ants in eastern Oregon and western Montana. Garton summarized relations between stand conditions and the abundance of predaceous birds in the mixed coniferous forests of northwestern states. Both Crawford and Jennings (northeastern states, U.S.A.) and Welsh (Ontario, Canada) summarized some of the responses by avian predators to forest composition in northeastern North America. As Garton pointed out, the economic value of these predators that has already been demonstrated suggests that deliberate efforts to increase predator populations may sometimes be cost effective.

Discussion Group A —
Parasites

Parasitoids of the Western Spruce Budworm in British Columbia

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In 1977, the western spruce budworm (*Choristoneura occidentalis* Freeman) caused serious defoliation of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) over 246 000 ha (607,866 acres), the largest area ever infested by budworm in British Columbia. The budworm was surveyed in 1977 and 1978, as the population declined (Harris and Dawson 1979).

Twenty-five parasitoid species were found, but only a few were abundant. Each budworm stage had a different parasitoid complex.

Early-stage larval parasitism averaged over 40 percent, and ranged from 21 to 100 percent at different locations. The most common species were *Apanteles fumiferanae* Viereck and *Glypta fumiferanae* Viereck, with only low numbers of five other species encountered. Late-stage larval parasitism averaged over 20 percent and ranged from 0 to 71 percent. Nine species of Diptera were found on this stage, the most common being *Ceromasia auricaudata* Townsend and *Winthemia fumiferanae* Tothill.

Total parasitism of both early and late instar larvae, calculated for 29 plots in 1977, averaged 54 percent, and ranged from 16 to 99 percent. In 1978, it averaged 59 percent over 20 plots, and ranged from 16 to 95 percent.

Pupal parasitism averaged 16 percent in 1977 and 25 percent in 1978, and ranged from 0 to 75 percent. Pupae were parasitized by the ichneumonids *Apechthis ontario* Cresson, *Itoplectis conquisitor* Say, *Itoplectis quadricingulata* Provancher, and *Phaeogenes hariolus* Cresson.

For 14 plots where both larvae and pupae were collected in 1977, total parasitism averaged 61 percent, and ranged from 58 to 99 percent. For 11 plots in 1978, parasitism averaged 69 percent, and ranged from 37 to 98 percent.

Egg parasitism by *Trichogramma minutum* Riley in 1977 averaged 17 percent for egg masses affected and 12 percent of total eggs. There was an average of 1.4 *Trichogramma* from each egg, compared to 2.1 reported by Wilkes et al. (1948) and 2.4 reported by Hewitt (1912).

A larval parasitoid not previously recorded for British Columbia on *C. occidentalis* was *Enytus* sp. Four others not identified but which could be new records were *Campoplex* sp., *Diadegma* sp., and specimens of Campopleginae and Porizontini. Hyperparasites were encountered in minor numbers: *Elasmus atratus* Howard parasitizing *G. fumiferanae; Mesochorus* sp. and *Mesochorus tachypus* Holmgren parasitizing *A. fumiferanae*; and *Mesopolobus* sp. attacking an unknown host.

Phytodietus fumiferanae Rohwer (Hymenoptera: Ichneumonidae) and *Cyzenis incrassata* Smith (Diptera: Tachinidae) were not found, although they had been collected by Wilkes et al. (1948) in large numbers for release in eastern Canada. The former had been collected by Silver (1960) near Pemberton, and the latter at Sumallo River near Hope in 1974. Neither species was collected by Doganlar and Beirne (1978) at Yale.

Total parasitism was 61 percent (1977) and 69 percent (1978); in 1977, 17 percent of the egg masses were attacked. Disease incidence was very low. The sudden decline of the budworm in 1978 over the entire infestation, regardless of parasitoid populations, suggested that parasitism was not a major factor. The widespread occurrence of parasitoids throughout the infestation suggests that they would not have been seriously affected overall by pesticide applications on limited areas.

Literature Cited

Doganlar, M.; Beirne, B.P. 1978. Natural enemies of budworms, *Choristoneura* spp. (Lepidoptera: Tortricidae), on Douglas-fir near Yale, British Columbia, in 1977. J. Entomol. Soc. B.C. 75:25-26.

Harris, J.W.E.; Dawson, A.F. 1979. Parasitoids of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia, 1977-78. J. Entomol. Soc. B.C. 76:30-38.

Hewitt, C.G. 1912. Some of the work of the Division of Entomology in 1911. 42nd Ann. Rept. Entomol. Soc. Ont. 1911:25-27.

Silver, G.T. 1960. Notes on a spruce budworm infestation in British Columbia. Forestry Chron. 36:362-374.

Wilkes, A.; Coppel, H.C.; Mathers, W.G. 1948. Notes on the insect parasites of the spruce budworm *Choristoneura fumiferana* (Clem.) in British Columbia. Can. Entomol. 80:138-155.

Percentage Parasitism of the Western Spruce Budworm: In Tree Crowns and following a Suppression Project

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Insect parasitism in the crowns of Douglas-fir and white fir was studied in northern New Mexico. Larvae were collected from the tips of branches in three crown levels of 8- to 16-m (26- to 52-ft) tall trees. Larvae were collected when most were either fourth stage or sixth stage. The larvae were reared until either moths or parasites emerged so that percentage parasitism could be calculated. Percentage parasitism then was analyzed for differences among aspects and crown levels.

Percentage parasitism for the more abundant braconid (*Apanteles, Meteorus*), ichneumonid (*Glypta, Phytodietus, Phaeogenes*), and tachinid (*Ceromasia, Madremyia*) parasites was not significantly different among aspects in either Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) or white fir (*Abies concolor* (Gord. and Glend.) Lindl.). Similarly, percentage parasitism was not significantly different among crown levels, except for *Meteorus* and *Glypta*. Many species were not abundant enough to determine if there were significant differences among aspects or crown levels.

In some cases, these results differed from the results reported by previous authors. The differences may have resulted from different methods of determining percentage parasitism, host dispersal, or different rates of mortality for parasitized and unparasitized larvae. A more detailed discussion is available in Schmid (1981a).

Parasitism after a Suppression Project

Insect parasitism was studied during and for 2 years after an insecticide suppression project in northern New Mexico. Budworm larvae were collected when fourth stage and sixth stage larvae predominated. The larvae were reared until either the adults or parasites emerged so that percentage parasitism could be calculated. Percentage parasitism was then compared between sprayed and unsprayed areas.

Percentage parasitism for most species changed insignificantly during the 2 years after insecticide application. Two species of ichneumonid parasites showed significant but opposite changes in percentage parasitism — *Glypta* decreased significantly; *Phytodietus* increased significantly. One species of braconid parasite, *Apanteles*, significantly increased in parasitism in some locations after spraying, although the overall change for this species for all locations was insignificant. *Apanteles* parasitism may increase during the first year or two after spraying, because host populations are reduced by the insecticide while the parasite is unaffected. Parasitism by the tachinid *Ceromasia* decreased significantly the first year after spraying, but parasitism was significantly greater in the sprayed area during spraying. Therefore, some of the change may have been influenced by sampling. More discussion and details regarding this study are available in Schmid (1981b).

Literature Cited

Schmid, J.M. 1981a. Distribution of western spruce budworm (Lepidoptera: Tortricidae) insect parasites in the crowns of host trees. (Can. Entomol. 113:1101-1106.

Schmid, J.M. 1981b. Incidence of western spruce budworm parasites in New Mexico after aerial spraying with carbaryl. U.S. Dep. Agric., For. Serv., Rocky Mt. For. and Range Exp. Stn. Fort Collins, CO. Res. Note RM-397. 6 p.

Discussion Group A —
Parasites

Parasitoids and Western Budworm Dynamics

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During population dynamics studies on the western spruce budworm (*Choristoneura occidentalis* Freeman) we collected detailed information on the parasitoids associated with this insect in the Pacific Northwest. Our objective was to examine the relation of parasitization to variation in budworm survival rates over a range of densities in widely scattered areas.

Between 1979 and 1981 we conducted intensive sampling and life table studies at 23 sites in Washington, Oregon, Idaho, and Montana. Budworm larvae, pupae and pupal exuviae, and egg masses were sampled on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) or grand fir (*Abies grandis* (Dougl.) Lindl.), or both.

Stage-specific mortalities caused by parasites, other natural enemies, and unknown sources were expressed in terms of k-values, i.e., killing power of various sources of mortality. The contribution of each mortality factor to generation change (K_G), or to population change from instar IV to adult (K_{L-A}) were examined in a manner similar to that of Varley and Gradwell (1960).

Egg mass densities among the populations varied from <1–70/m^2 (10 ft^2). Egg parasitization was low, averaging only about 1 percent. Instar IV densities varied from <1–48/m^2 (10 ft^2); two-thirds of the populations had fewer than 20 larvae/m^2 (10 ft^2). Larval parasitization was 7–44 percent ($\bar{x} = 17$ percent). Group means for larval parasitization among increasing outbreak, stable outbreak, and decreasing outbreak populations were significantly different. Parasitization in stable sparse populations was significantly lower than that observed in declining outbreaks, but did not differ from increasing or stable outbreaks.

Parasitization of pupae varied between 0 and 59 percent ($\bar{x} = 16$ percent) in populations with densities of <0.1–23 pupae/m^2 (10 ft^2). Pupal parasitization among declining outbreak populations was significantly higher than the other three categories of populations.

Mortality of larvae and pupae from parasites constituted about 24 percent of deaths during the period from instar IV to adults. Among stable populations, larval and pupal parasites contributed about equally to K_G (2.0 and 2.7, respectively). Among increasing and stable outbreak populations, larval parasites contributed most to variation in K_G (4.2 *vs* 2.4 percent of K_G, respectively). Parasites that killed pupae had the greatest effect among declining outbreak populations. The contribution of parasitization to mortality during the generation (K_G) was about 9 percent overall. Thus, mortality factors other than parasites accounted for about 91 percent of the variation in K_G.

The contribution of parasitization to K_{L-A} was about 15 percent at increasing outbreak sites in Oregon and Montana, yet budworm populations have continued to increase. In Washington, where populations had been decreasing for several years, parasitization contributed about 48 percent to variation in K_{L-A}, and about 19 percent to K_G. This suggests that parasites were exploiting already diminishing numbers of hosts and thereby reinforcing the population collapse.

In studies designed to examine the role of insectivorous birds and foliage-foraging ants on budworm numbers, we found that these predators contributed about 29 percent to variation in K_G. When both of these predator guilds were excluded from trial trees, all the other mortality factors, including parasites and other predators, contributed relatively little to mortality. More significantly, these other mortality agents did not exhibit any apparent compensatory reaction to the absence of the excluded predator guilds by increasing their own activity (Campbell and Torgersen 1983).

Our studies suggest that parasitization contributed little to variation in survival rates from instar IV to adults, or overall during the generation. Also, parasites are apparently slow to respond to increases in available hosts. We believe our data indicate that over a broad range of densities in a major portion of the budworms distribution, parasitization may have a lesser role in the insects dynamics than earlier figures on percentage of parasitization alone have suggested (Torgersen et al. 1984).

Parasite Species Obtained from Western Budworm

Fourteen species of parasites were consistently represented in our rearings. The species are listed in approximate order of decreasing dominance: *Apanteles fumiferanae* Viereck, *Glypta fumiferanae* (Viereck), *Charmon gracile* (Provancher), *Enytus montanus* (Ashmead), and *Mesochorus tachypus* Holmgren (a secondary parasite), were all from larvae. Species reared from pupae were: *Agria housei* Shewell, *Madremyia saundersii* (Williston), *Ceromasia auricaudata* Townsend, *Phaeogenes maculicornis hariolus* (Cresson), *Itoplectis quadricingulata* (Provancher), *Ephialtes ontario* (Cresson), *Phorocera incrassata* Smith, and *Timavia fumiferanae* (Tothill). *Trichogramma minutum* (Riley) was the only parasite reared from budworm eggs.

Literature Cited

Campbell, R.W.; Torgersen, T.R. 1983. Compensatory mortality in defoliator population dynamics. Environ. Entomol. 12:630-632.

Torgersen, T.R.; Campbell, R.W.; Srivastava, N. 1984. Role of parasites in the population dynamics of the western spruce budworm (Lepidoptera: Tortricidae). Environ. Entomol. 13:568-573.

Varley, G.C.; Gradwell, G.R. 1960. Key factors in population studies. J. Anim. Ecol. 29:399-401.

Discussion Group A — Parasites

Spruce Budworm Parasitoid Surveys in Ontario

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The Forest Insect and Disease Survey (FIDS) is an operational unit within the Canadian Forestry Service associated with each of the six regional forest research centres throughout the country. The primary objectives of FIDS are to determine the distribution of native insects and their damage and to detect changes in population or damage levels of certain forest pests. In Ontario, the FIDS unit, of the Great Lakes Forest Research Centre in Sault Ste. Marie, has been heavily involved in monitoring the current spruce budworm outbreak. Staff of this unit have also been involved in planning, timing, and assessing aerial control operations carried out against the budworm by the Ontario Ministry of Natural Resources (OMNR). An intensive effort has not been put into budworm parasitoid research; however, the unit has conducted special parasitoid surveys and has participated in experimental releases of the budworm egg parasite *Trichogramma minutum*. Summaries of these activities are presented in this report.

Parasitoid Surveys

Trichogramma minutum: Since 1967, when the current spruce budworm outbreak began in Ontario, the FIDS unit has conducted an annual budworm egg-mass survey involving as many as 650 locations throughout the province. During examination of the foliage samples, healthy and parasitized egg masses were recorded (egg masses are counted as parasitized if >50 percent of the mass is parasitized). In 1982 and 1983 a preliminary examination of this 15-year data package was carried out. Summaries were prepared on an OMNR district, region and geographic basis, and correlations were calculated for a number of relationships. Analysis of this data is far from complete, but a few generalizations are possible. It does appear that there are geographic limitations to the distribution of *T. minutum*. It is nonexistent or rare in the more northerly portions of the budworm outbreak and appears to become progressively more abundant the further south one goes. In regions where *T. minutum* is relatively abundant it appears to show a limited numerical response to fluctuations in budworm egg-mass densities. A more in-depth analysis of this data is planned for the near future.

Infestation Age and Spruce Budworm Parasitism

It has been suggested that spruce budworm outbreaks are initiated by moth flights from established infestations to stands a considerable distance away. If this does occur, the parasitoid complex in these new or so-called "secondary infestations" should differ, both in numbers and species diversity, from those in older infestations. In 1983, FIDS staff began a special survey to examine the relationship between the incidence of budworm parasitism and the age of the infestation. Larval and pupal collections were taken from three sites in northwestern Ontario, each representing a different-aged infestation — 1-, 3-, and 9-years old. The larvae and pupae were reared and emerging parasitoids identified. A greater diversity of parasitoids emerged from the collections from the two older infestations, but the levels of parasitism were not determined. This survey will be repeated in 1984.

Spruce Budworm Parasitoids in Sprayed and Unsprayed Stands

Each year since 1968, OMNR has conducted an aerial spraying program somewhere in the province of Ontario against the spruce budworm. In 1983, FIDS conducted a survey to assess the impacts of spraying on budworm parasitoids. Three areas in Rogers Township, Hearst District were chosen for the survey; one area was treated with Matacil® 1.8F (90 g/3.0 L/ha, 1.27 oz/0.3 gal/acre) the second with Dipel® 88 (30 BIU/3.5 L/ha, 12 BIU/0.37 gal/acre), and the third was untreated. Results based on an examination of budworm larvae and pupae collected from the treated and untreated areas, were inconclusive. This survey will be repeated in 1984.

Experimental Releases of *Trichogramma minutum*

In 1982, OMNR initiated a series of experimental trials involving small scale ground and aerial releases of the budworm egg parasite *Trichogramma minutum*. The trials were conducted in several white spruce plantations in Rogers Township, Hearst District where budworm populations were stable and the incidence of natural *T. minutum* parasitism was extremely low. The 1982 trials were hampered when problems arose in the parasite rearing facility at the University of Guelph. Consequently the application rates were reduced (250,000 ♀/ha [101,173 ♀/acre] in the aerial release plot and 480,000 to 12.0 million ♀/ha [194,253 to 4.85 million ♀/acre] in the ground release plots); parasitism levels were low. The program was repeated in 1983 but with higher application rates (16.5 million ♀/ha [6.7 million ♀/acre] in the aerial release plot and three applications of 12.0 million ♀/ha [4.85 million ♀/acre] in the ground release plots). FIDS staff surveyed the release plots in August and found parasitism levels of 22 to 25 percent in the aerial release stand and 41 to 64 percent in the ground release stand. A third trial is planned for 1984.

Discussion Group A — Parasites

Summary

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From the discussions during the symposium and the preceding abstracts, it is evident that most of the research supported by the CANUSA Spruce Budworms Program on the role of parasites in the population dynamics of the spruce budworm was conducted in the western United States and Canada on *Choristoneura occidentalis*.

During the meeting T.R. Torgersen reported on the relationship of parasitism to variation in budworm survival rates over a range of budworm densities. Although not in attendance, several other scientists provided abstracts of their work. J.M. Schmid's abstract gives information on parasitism in tree crowns and parasitism rates following an insecticide suppression project. The abstract by J.W.E. Harris and A.F. Dawson provides a summary of rates of parasitism by various species in British Columbia. The only abstract dealing with *C. fumiferana* was submitted by J.H. Meating, G.M. Howse, P.D. Syme, and K.L. Smith, and covers parasite surveys and *Trichogramma* research projects in Ontario. The *Trichogramma* projects are described in further detail under Session 2 — J.R. Carrow, S.A. Nicholson, and S. Smith in Workshop IV, "Techniques of foliage protection and population manipulation."

Discussion Group A — Diseases

Epizootic Development of Entomophthoralean Fungi

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Fungal disease occurs throughout the life-cycle of the spruce budworm. Of the six or so fungi commonly infecting *C. fumiferana*, two entomophthoralean species, which appear during the fifth and sixth instar, can cause epizootics: *Erynia radicans* and *Entomophaga aulicae*. Although all stages are susceptible, the annual infection cycle begins with fifth instar larvae, even when fungal incidence is very low. This synchrony is best attributed to the relationship between temperature and development. Insect movement from tree to tree or from the canopy to the soil and back again aids in spreading the disease and may provide the impetus for an epizootic during wet periods. In northern Ontario it is probable that dewfall alone can supply sufficient moisture. In addition, long-term annual accumulation of inoculum does not seem to be a prerequisite for an epizootic. In the year prior to high fungal incidence, infection levels can be lower than 5 percent.

The transition from enzootic to epizootic is marked by the beginning of secondary inoculum production. In other words, initial infections are the result of the host encountering a conidium stemming from an overwintering source, either germinating resting spores or conidia. Within a day of death a cadaver may sporulate, producing about 1 million conidia over the next 48-hour period. This exponential increase in conidia is responsible for the epizootic; in overview, the factors leading to high levels of mycosis include:

- a fungal inoculum
- the host
- an initial encounter between host and overwintering spores
- larval movement
- humidity

It is possible to speculate about a relationship between inoculum and host densities, or larval numbers and movement leading to infection, or the duration of wetness required to initiate an epizootic. However, the importance of each of these factors and the minimal thresholds of inoculum density, host numbers, movement, and humidity must be determined. Probably there is compensation amongst these criteria and a single set of conditions will not be preordained.

An epizootic can cover a large area of forest; high levels of mycosis have been observed over 800 km^2 (309 mi.^{2}), although within this area, infection can be very spotty. Such heterogeneity describes fungal distribution in general, even in a single tree and especially when infection is rare. The impact of mycosis on spruce budworm populations would be a result of the timing and intensity of infection. Microbial reproduction and movement would also make it possible for waves of infection to occur, both seasonally and annually. Infective spores are forcibly projected and transported by the wind for distances of several hundred kilometres. Therefore, reservoirs of epicenters of infection can be responsible for the disease detected in outlying areas (Do conidia follow budworm moth flight?). This might happen during an epizootic where large numbers of conidia are formed.

Within the forest there are alternate hosts for both *E. radicans* and *E. aulicae*, and epizootics on these insects also occur (e.g., hemlock looper). Fungi infect all orders and may contribute to the regulation of many different insect populations; however, because of the complex relationship between these microbes and their hosts, discussions are limited to the effects of mortality on a percentage population basis.

As was discussed earlier, it is difficult to assess the impact of a particular percentage mortality. The percentage of insects actually succumbing to mycosis involves a consideration of infection, incubation and transmission times. Ultimately, competition between microbial pathogens, parasites and predators may also be important. Mycosis caused by entomophthoralean fungi can infect over 95 percent of a localized insect population. It remains to be seen what this level of mortality during the fifth and sixth instar means in terms of long-term budworm dynamics.

Discussion Group A —
Diseases

The Role of Infectious Disease in the Population Dynamics of the Spruce Budworm (*Choristoneura fumiferana*)

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The spruce budworm hosts a number of infectious disease organisms including at least three species of Microsporidia (Protozoa), many virus groups, several fungal species, bacteria, and probably other less evident microbes. These microparasites rely on a cycle of reproduction for their persistence within diseased hosts followed by infection of new individuals (transmission). The budworm is a difficult host for microparasites to contend with because of various characteristics of its life-history. Larvae are virtually hidden until budflush by which time they have reached the fourth instar or beyond, and even then, physical contact between larvae is limited except in dense populations. Thus, transmission of infective propagules between larvae is restricted until the fourth instar and rapid reproduction of infective propagules is required within the larvae to produce more generations before pupation. Non-overlapping generations of the budworm and severe winters also pose problems; the unique microbial responses include persistence in alternate hosts, persistence in durable "resting" propagules, and transmission from moth to egg.

Nosema fumiferana is the most prevalent microsporidian; *Pleistophora schubergi* and *Thelohania* spp. are less frequent. *Nosema* occurs in all budworm life stages, potentially reducing adult fecundity and killing larvae when spore loads are high. Transmission between larvae, through alternate hosts, and from moth to egg are possible means of increasing the incidence of *Nosema* in budworm populations.

Four different insect virus groups have been isolated from budworm: granulosis, nuclear polyhedrosis, entomopox, and cytoplasmic polyhedrosis. These viruses rely on interlarval transmission which can be very inefficient because of the extreme sensitivity of infective propagules to heat and UV light. These viruses commonly infect a small part (less than 5 percent) of the population but natural epizootics have not been reported. Virus in nonoccluded or latent forms is extremely difficult to detect and this may help explain the lack of reported natural epizootics.

Among budworm's fungal pathogens, the imperfect fungi (*Beauveria*, *Hirsutella*, *Isaria*, and *Metarrhizium*) are less prevalent than the Entomophthoralean species (*Conidiobolus* spp., *Erynia radicans*, and *Entomophaga aulicae*) but, excepting *Hirsutella gigantea* and *Isaria farinosis*, seem to exist in highest numbers on pupae. In contrast, *E. radicans* and *E. aulicae* may cause high mortality of fifth and sixth instar larvae, perhaps as a result of their ability to reproduce infective inoculum rapidly. Overwintering occurs most successfully as resting spores; alternate hosts may be present but moth to egg transmission does not occur.

The bacterial pathogen *Bacillus thuringiensis* also infects budworm. Spores persist well in the soil despite competition with other soil organisms, and a limited range of alternate hosts are available. However, natural bacterial epizootics are rare, presumably because of the low number of new infective agents produced in a cadaver.

Together, these microparasites, whether artifically introduced or naturally occurring, play a role in budworm dynamics. To do so they must interact amongst themselves as well as with other components of the forest. For instance, there are indications of synergistic effects between some microsporidia (Wilson 1981) and of competitive effects among viruses as well as between virus and *B. thuringiensis* (Jaques and Morris 1981). There are also suggestions that parasitic insects may transmit *N. fumiferana* during oviposition (Wilson 1982), that the larvae of parasitic insects may acquire lethal doses of *N. fumiferanae* from infected hosts (Wilson 1981), and that some foliar exudates may harm *B. thuringiensis* spores (Jaques and Morris 1981). Such potential complexities make it difficult to define precisely the role of infectious disease in budworm population dynamics.

Recent work in budworm population dynamics, however, has created a surge of interest in the role of disease. Royama (1984) implies that disease may be driving periodic 30-40 year oscillations of budworm populations. He suggests that certain microparasite populations may rise in response to budworm concentrations, limiting outbreaks. Subsequent collapse then theoretically deprives these microparasites of their hosts and disease populations decline soon afterwards. A pattern of oscillations in population sizes typical of predator-prey relationships is expected. The data displayed in Figure 1 may be consistent with this idea. On the other hand, these data may also be consistent with 1) a one-way cause and effect relationship whereby *Nosema* numbers change in response to, but have no important affect on, changes in budworm densities (or vice-versa), and 2) the absence of any causal interdependence: cycles in budworm densities and *Nosema* incidence just happened to be aligned in this particular pattern from 1953-1984.

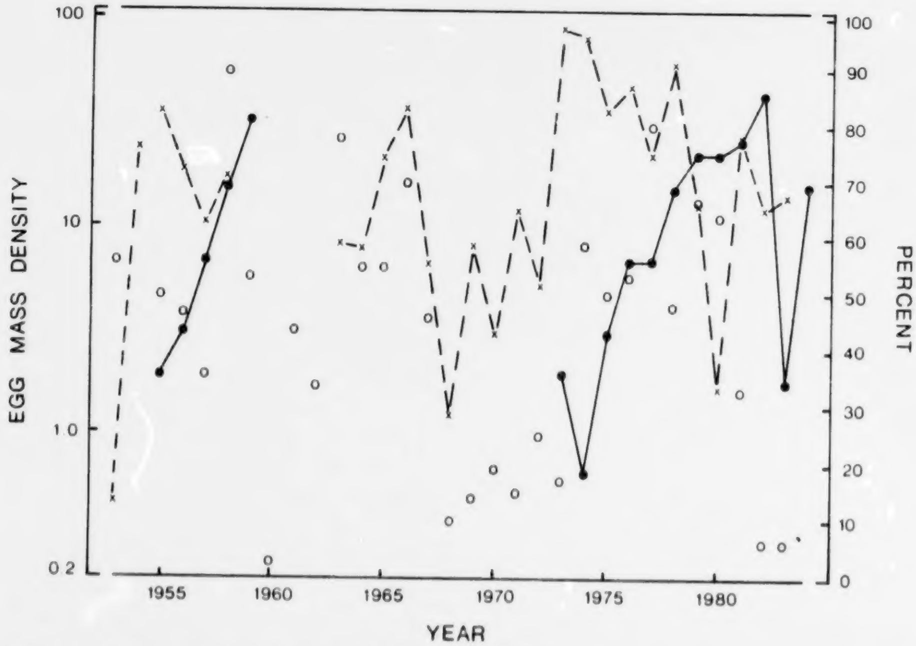

Figure 1. Percent budworm infected by *N. fumiferanae* (o–o), percent current defoliation (0), and spruce budworm egg mass density (x–x) in a white spruce (*Picea glauca*) plot near Uxbridge, Ontario. Egg mass densities were measured as number per full branch in 1953-1954 and number per m² of foliated branch surface thereafter. (Data provided by G.G. Wilson and G.M. Howse, Canadian Forestry Service, Sault Ste. Marie, Ont.)

Literature Cited

Jaques, R.P.; Morris, O.N. 1981. Compatability of pathogens with other methods of pest control and with different crops. Pages 695-715 *in* H.D. Burges, ed. Microbial Control of Pests and Plant Diseases, 1970-1980. Academic Press, London.

Royama, T. 1984. Population dynamics of the spruce budworm, *Choristoneura fumiferana* (Clem.): A reinterpretation of life table studies from the Green River Project. Ecol. Monog. 54(4):429-462.

Wilson, G.G. 1981. *Nosema fumiferanae*, a natural pathogen of a forest pest: potential for pest management. Pages 595-601 *in* H.D. Burges, ed. Microbial Control of Pests and Plant Diseases, 1970-1980. Academic Press, London.

Wilson, G.G. 1982. Protozoans for insect control. Pages 587-600 *in* E. Kurstak, ed. Microbial and Viral Pesticides. Dekker, New York.

Discussion Group A —
Diseases

Infectious Diseases as Part of the Group of Mortality Factors Affecting Eastern Spruce Budworm Population Dynamics

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A common temptation is to consider the mortality factors affecting a population on an individual basis, as though each operates independently of all others. For the spruce budworm (*Choristoneura fumiferana*), it may be more appropriate to view many of its predators, parasites, and diseases as mutually interacting and interdependent elements of a complex of natural enemies.

This interdependence and mutual interaction of infectious diseases is most evident during transmission. Figure 1 illustrates the processes involved in disease transmission in general, and for budworm fungal pathogens in particular. Infective spores are actively projected into air currents from budworm cadavers. For infection to occur, a spore must contact a budworm, penetrate the cuticle through germination, and grow within the insect. Shortly after the insect's death, the next generation of infective spores is released. The critical step in disease transmission is the contact between a budworm and the infective inoculum which depends on budworm density and activity, and both of these, in turn, can be affected by other mortality factors. For instance, if egg and small larval mortality caused by *Nosema fumiferana* is high, large larval densities may be low and thus restrict the spread of the Entomophthoralean fungi later in the season. Similarly, feeding inhibition caused by *Bacillus thuringiensis* may reduce the ingestion of *Nosema* spores by budworm and thus limit *Nosema* incidence. Hence, interdependence of disease-caused budworm mortality occurs on both a contemporary and a sequential basis. Ultimately, budworm predators, parasites, and pathogens are all competing over a common resource: individual insects.

Interdependence of mortality factors is also evident in budworm generation mortality. Because a mated female lays about 200 eggs, generation mortality must approach 99 percent to prevent population increase. Mathematically the number of mature moths surviving from these 200 eggs can be expressed as:

$$N = 200 \times (1\text{-}E)(1\text{-}S)(1\text{-}L)(1\text{-}M)$$

where E, S, L, and M are the stage specific mortality rates for eggs (E), small larvae (S), large larvae (L), and pupa-moths (M). Typical values might be E = 0.2,

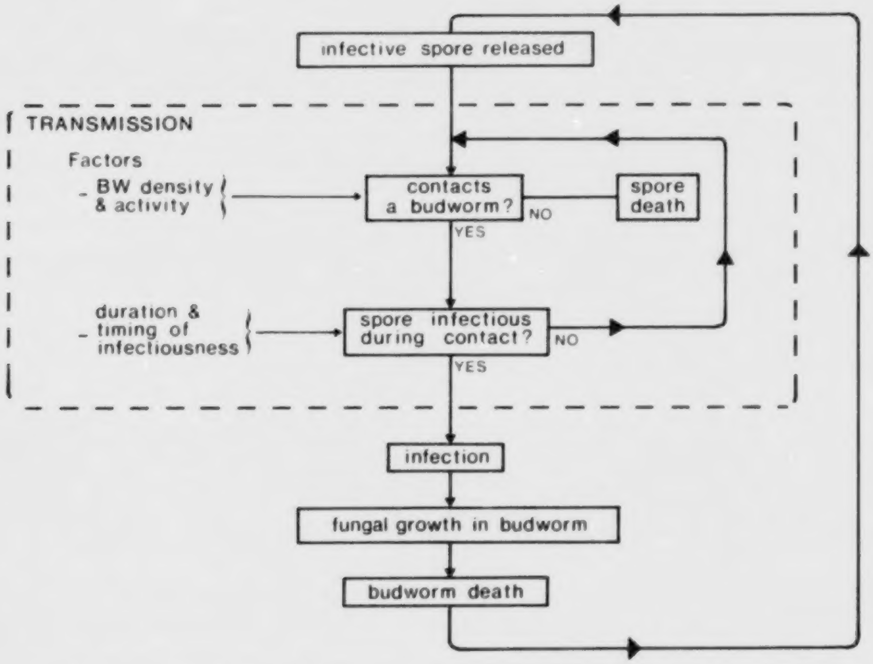

Figure 1. Diagram of the process of recurrent fungal infection of the spruce budworm. The broken line encloses the steps involved in transmission and, to their left, the major factors affecting these steps.

S = 0.8, L = 0.9, and M = 0.375, which results in N = 2 surviving mature moths or just enough, on average, to replace the one mated female of the previous generation.

This equation also emphasizes the nonadditive relationship between the effects of mortality occurring at different life stages. For example, changing egg mortality by 5 percent to E = 0.15 or 0.25 and keeping all other values as above, results in N = 2.12 or 1.88 surviving mature moths, respectively. Given these changes, the budworm population would double in 11.4 years or halve in 10.7 years, respectively. In contrast, holding egg mortality at E = 0.2 and changing large larval mortality by 5 percent to L = 0.85 or 0.95, results in N = 3 or 1 surviving mature moths, respectively. This has much more drastic consequences: the corresponding budworm populations double every 1.7 years or halve every year, respectively. At this rate, these populations would be over 100 times larger in 12 years or under 100 times smaller in 7 years! Hence, as a consequence of the nonadditivity of stage specific mortalities, small changes in seemingly unimportant mortality factors can have important effects, especially when they occur during life history bottlenecks (life stages where total mortality is high).

This conclusion implies that breakthroughs in our knowledge of many budworm mortality factors may not come until such factors are examined in the context of the "background" mortality with which they coincide. For this reason, broad-based ecological approaches to field studies of budworm mortality factors seem most promising.

Discussion Group A — Diseases

Summary

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There are more than 15 reported diseases of spruce budworm (*Choristoneura fumiferana* (Clem.)). The two most prevalent include the microsporidian, *Nosema fumiferanae* and fungi of the Entomophthorales (Zygomycotina). These microorganisms have very different life-cycles although in terms of pathology a common development pattern is shared: infection, reproduction, transmissions, and persistence.

The generation time, or period necessary for completion, of the infection-transmission cycle varies and is weather dependent. For the Entomophthorales an average duration would be 3-5 days, but with *Nosema*, the time is indeterminate. This phenomenon bears strongly on the ability of a pathogen such as *Nosema*, which is not always lethal, to influence its host. The effect of *Nosema* on a budworm population is not wholly accounted for by a percentage mortality estimate, but rather by a combination of mortality and sublethal effects. The fungi, however, are lethal.

The timing of infection (effect) is also important, as mortality is not additive. An agent that occurs early in the cycle of the insect will certainly influence the amount of susceptible individuals available later on. Small changes in percentage mortality can represent dramatic differences in host survivorship over the long term. The interrelationships between diseases will need to be clarified before their role in population regulation will be discernable.

Epizootics due to entomophthoralean fungi are the result of secondary infections beginning with an in-season inoculum. The overwintering spores, whether resting spores or conidia, maintain the disease at low levels. Infection is delayed until fifth instar in a given season because of the necessity for an infective inoculum to accumulate. At this point, larval movement during late instars increases encounters with conidia and aids in the dissemination of the disease from the forest floor and throughout the canopy. Long distance dispersal of spores during an epizootic spreads mycosis to outlying areas. Epizootics do not necessitate long-term annual buildup of inoculum, but rather represent the coincidence of appropriate humidity, larval densities, and a minimal fungal inoculum. The exact requisites for each are probably not preordained, but all the above factors certainly play a role.

Discussion Group A —
Budworm Behavior

Second Diapause in the Population Dynamics of Spruce Budworms

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In the analysis of the population dynamics of *Choristoneura biennis* and *C. orae*, the importance of second diapause must be recognized as a normal part of the life cycle. In both these species, which inhabit the higher latitudes and elevations of central and northern British Columbia, development is interrupted by periods of diapause in both the second and fourth instars. In laboratory rearings of progenies of field-collected *C. biennis*, virtually all larvae enter second diapause even though conditions are favorable for uninterrupted development. The second diapause in this species is therefore considered to be genetically fixed (Harvey 1967).

The incidence of second diapause in laboratory rearings of *C. orae* was reported as 82 percent (Harvey 1967). Progenies of *C. orae* collected in Anchorage, Alaska in 1979–1981 had 67.8 percent second diapause. In this species there is considerable variation among families, percentage second diapause ranging from 13 to 100 percent. Thus second diapause is probably not firmly fixed genetically, but is susceptible to influence by environmental conditions (Harvey 1967).

Incidence of second diapause among the other *Choristoneura* species is very low. Values of 1.7 percent for *fumiferana* and 4.1 percent for *occidentalis* were reported in laboratory rearings (Harvey 1967). In both species the percentage second diapause is influenced by length of photoperiod and by unfavorable diet (Harvey 1967). Relative humidity during egg development, temperature, and length of overwintering storage also influence the incidence of second diapause in *fumiferana* (McMorran 1972).

Second diapause levels in progenies of collections from the northwestern parts of the distribution of *C. fumiferana* are greater than reported for eastern Canada. In 15 collections from north of latitude 55 °N and west of longitude 100 °W, second diapause averaged 8.6 percent. Higher levels of second diapause may also be present at the northern parts of the distribution of *C. occidentalis*.

Most of the above information on second diapause is based on laboratory data. Nevertheless, second diapause may occur naturally in all species. Second diapause larvae were reported in insectary rearings of *C. fumiferana* (I.M. Campbell, personal communication). And recently T. Egan (personal communication) found about 2 percent second diapause larvae during spring emergence of *C. occidentalis* from log bolts in north-central Washington. The existence of surviving second diapause larvae during spring emergence of *C. fumiferana* and *C. occidentalis* is difficult to establish because of the very low numbers and the difficulty of positive identification of very small larvae. Furthermore, the timing and patterns of emergence may not be the same as for the first diapause. The earlier conclusion that both *fumiferana* and *occidentalis* possess some tendency to enter second diapause (Harvey 1967) still appears to be valid even though natural levels of expression are very low.

Conditions for fulfilment of second diapause in *C. biennis* and *C. orae* appear to be generally similar to those for the first diapause (Harvey 1958) although minimum storage times may be longer. In laboratory rearings overwintering survival is generally high and subsequent development rapid. For example, of 172 larvae of *C. orae* (progeny of 1981 collection) stored at 1.2 °C (34 °F) for 38 weeks, 90 percent emerged and 82 percent of these became adults. Similar results have been obtained with *C. biennis*. Data are scarce for the other *Choristoneura* species, including *fumiferana* and *occidentalis* because of the low frequencies of second diapause, but the levels of survival to adult appear similar.

Because of its low frequency, second diapause is probably of little significance for the population dynamics of *C. fumiferana* and *C. occidentalis* through most of their distribution. The incidence of this behavior may be greater at the present northern limits of both species and it may at times contribute to population survival and stability during periods of adverse weather. The existence in these two species of some tendency to second diapause undoubtedly reflects their history and their relationship to the two western species that continue to rely on second diapause for generation survival.

Literature Cited

Harvey, G.T. 1958. A relationship between photoperiod and cold storage treatment in the spruce budworm. Science 128:1205-6.

Harvey, G.T. 1967. On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. V. Second diapause as a species character. Can. Entomol. 99:486-503.

McMorran, A. 1972. Effects of some environmental factors on the occurrence of second diapause in laboratory-reared *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 104:1649-1653.

Discussion Group A —
Budworm Behavior

Sex Pheromone as a Trigger of Female Moth Dispersal

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The intensive study of budworm moth dispersal in New Brunswick, 1973-76, generated considerable information on factors affecting dispersal and the displacement of airborne moths. An unanswered question, which has since been shown to be of potential significance in population dynamics, is whether dispersal is density dependent.

To answer this, we have observed moth behavior for a number of years at different population densities in Ontario. The results are summarized in Figure 1. Our conclusion is that dispersal is related to density. The most convincing evidence is from Black Sturgeon Lake, northwestern Ontario, where observations have been the most intense and complete; dispersal was seen only when defoliation (and hence population density) increased dramatically in 1982. In Searchmont and Swallow Lake, dispersal was associated with heavy defoliation. An exception appears to be Aldina in 1976, but 60 percent defoliation leaves much green foliage, and the trees were in good health.

Assuming dispersal is density dependent, what factor triggers it? One possibility is high concentrations of pheromone. Budworm females can perceive their own pheromone (Palanaswamy and Seabrook 1978). We have therefore monitored activity of mated female moths in pheromone-permeated and clean air, using a 30- × 30- × 30-cm (12- × 12- × 12-in) Faraday cage in which a flying moth creates a measurable electrostatic disturbance. Results (Figure 2) show that the moths are far more active in pheromone-permeated air, which suggests dispersal would increase.

Observations in the field do not support this, however. On three occasions (at Black Sturgeon Lake 1977, at

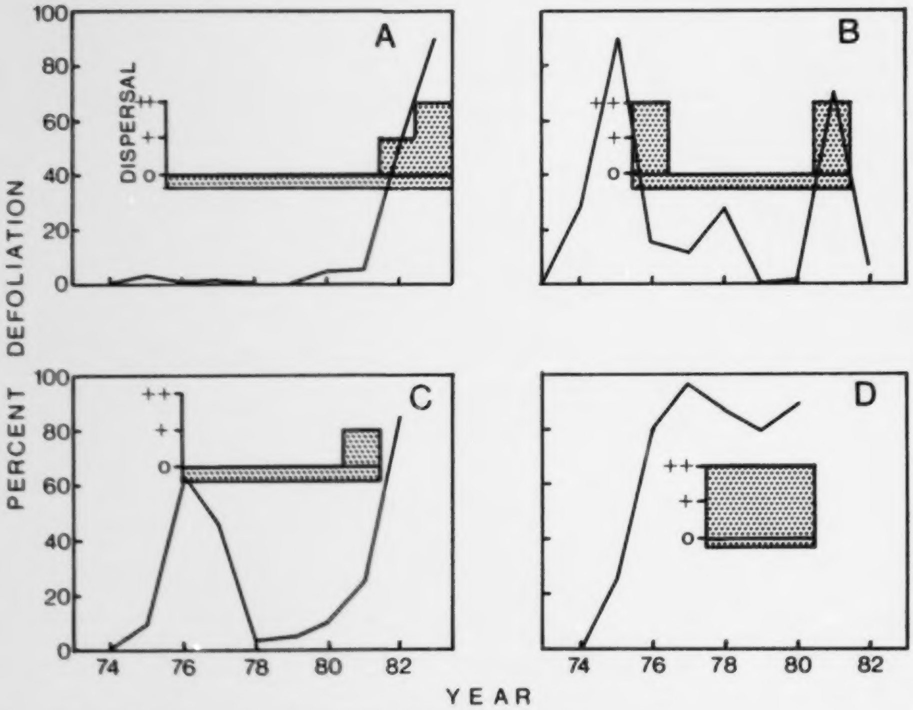

Figure 1. Relation between defoliation and dispersal of female spruce budworm moths in four areas of Ontario (A = Black Sturgeon, B = Searchmont, C = Aldina, D = Swallow Lake). Shaded area denotes years in which observers watched for dispersal, 0 = no dispersal seen, + = a few dispersing, ++ = heavy dispersal.

Searchmont 1977, and at Kirkwood 1981), we have applied large amounts of synthetic pheromone to field populations in an attempt to disrupt mating. Although male catches in pheromone-baited traps were greatly reduced — implying that the pheromone was present — no dispersing females were seen even though observations were made each night from scaffolds above the tree canopy throughout the moth flight.

We therefore conclude that although moth dispersal is density dependent, evidence for pheromone as the triggering mechanism is inconclusive.

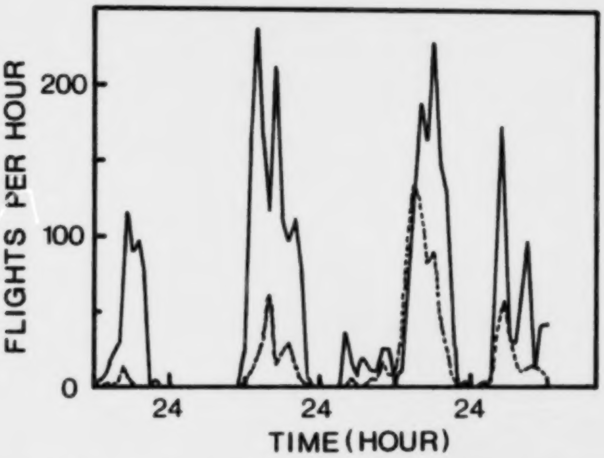

Figure 2 Flight activity of mated female spruce budworm in "clear air" (dotted line) or in pheromone-permeated air (solid line), measured in an activity chamber 30 × 30 × 30 cm (12 × 12 × 12 in).

Literature Cited

Palanaswamy, P.; Seabrook, W.D. 1978. Behavioral responses of the female eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae) to the sex pheromone of her own species. J. Chem. Ecol. 4:649-655.

Discussion Group A —
Budworm Behavior

Strip Clearcutting Contributes to Dispersal Losses of Early-Instar Spruce Budworm Larvae

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Numerous factors affect early-larval dispersal of the spruce budworm, including characteristics of forest stands. Dispersal losses are relatively low in dense stands of preferred host trees but relatively high in open stands or mixed-wood stands (Morris and Mott 1963). Because strip clearcutting opens forest stands, permitting greater air movement and an abundance of nonhost vegetation (*Rubus* spp.), we postulated that this harvesting practice influences early-larval dispersal of the spruce budworm.

We investigated dispersal losses of first (L_1) and second instars (L_2) in five strip clearcuts and five nearby dense (control) spruce-fir stands of northern Maine. To capture dispersing larvae, we used sticky-board traps with protective screens (Jennings and Houseweart 1983). Egg populations were estimated from 20 host-tree branches/plot to determine numbers of larvae available for dispersal. Egg and larval densities per square metre were converted to absolute populations per hectare.

Significantly more L_1 larvae were trapped in uncut residual strips than in dense stands, but not in cut strips. Significantly more L_2 larvae were trapped in cut strips than in residual strips or dense stands. Consistently more L_2 larvae were caught than L_1 larvae. Mean percentages of $L_1 + L_2$ larvae trapped represented small fractions (1.4 to 4.0 percent) of initial egg populations.

Although more eggs were sampled per square metre of foliage in residual strips, absolute populations per hectare were not significantly different between dense stands and residual plus cut strips (Table 1). Numbers of trapped L_1 larvae also did not differ significantly for the two forest conditions, but noticeably more L_2 larvae were trapped in strip clearcuts (residual plus cut strips) than in dense stands (Table 1).

These results indicate that strip clearcutting contributes substantially to dispersal losses of early-instar larvae of the spruce budworm (Jennings et al. 1983). Estimated combined losses ($L_1 + L_2$) were 1.4 million larvae per hectare (567,000 larvae per acre) for dense stands and 2.9 million larvae per hectare (1.18 million larvae per acre) for strip clearcuts; however, such losses may be insignificant in terms of overall generation survival.

Table 1
Mean absolute populations per hectare by spruce budworm life stage and forest condition

	Forest condition	
Life stage	*Dense stands*	*Residual + cut strips*^{1}
Eggs	*114 769 030*	*87 120 910*^{NS}
L_1 larvae	*170 370*	*297 685*^{NS}
L_2 larvae	*1 288 869*	*2 676 541**
$L_1 + L_2$ larvae	*1 459 240*	*2 974 266***

^{1}^{NS} not significant (P = 0.05). * significant (P = 0.05). ** significant (P = 0.01.)

Literature Cited

Jennings, D.T.; Houseweart, M.W. 1983. Sticky-board trap for measuring dispersal of spruce budworm larvae. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Stn., Broomall, Penn. Res. Pap. NE-526. 7 p.

Jennings, D.T.; Houseweart, M.W.; Dimond, J.B. 1983. Dispersal losses of early-instar spruce budworm (Lepidoptera: Tortricidae) larvae in strip clearcut and dense spruce-fir forests of Maine. Environ. Entomol. 12:1787-1792.

Morris, R.F.; Mott, D.G. 1963. Dispersal and the spruce budworm. Pages 180-189 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332 p.

Discussion Group A —
Budworm Behavior

Dispersal of Western Spruce Budworm Larvae and Adults as related to Silvicultural Treatments

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Silvicultural practices alter the forest environment, usually creating better growing conditions for crop trees and newly regenerating stands. Often, these practices also create an environment less favorable for the western spruce budworm. Foresters are intensely interested in this approach because it not only modifies the insect habitat but also the effects are long term compared to the short term effect of treatments applied directly to the target insect.

One aspect of western budworm behavior affected by a change in the habitat produced through silviculture is the dispersal of larvae and adults. For more than a decade, we have been studying how local dispersal is affected by several different silvicultural systems, intensities of treatment, sizes of cutting units, and varieties of forest types.

We have used an 18- × 24-in (46- × 61-cm) sticky trap covered with a mesh screen, held about 1 foot (0.3 m) above the ground on three legs (Figure 1). These traps are deployed in a grid system throughout cutting units and adjacent undisturbed forests (Figure 2).

The effects of clearcutting on larval dispersal have been variable. In 1973, we found that the number of second instars that dispersed in the spring was 10 times greater in undisturbed forests than in adjacent clearcuts of 125 acres (50 ha) or larger. This relationship was similar for summer-dispersing first instars, but the magnitude of difference was not as large with 4 times more larvae dispersed in the undisturbed stands as shown below:

	Dispersing budworm larvae	
	Undisturbed forest	*Clearcut*
	larvae/m²	
Spring 1973	*150*	*15*
Summer 1973	*10*	*2.5*

In smaller clearcut units of about 15 acres (6 ha), we consistently found populations of spring-dispersing larvae to be higher in the cutting units than in the adjacent undisturbed forest, where populations average about 225 larvae/m² (21 larvae/ft²). Our more recent research in different forest types showed little difference in the number of larvae dispersing into clearcut units, regardless of size, compared to the adjacent undisturbed stands.

We nearly always found significantly more larvae dispersing to the forest floor in partial cut silvicultural systems — such as shelterwood or seed-tree cuts —

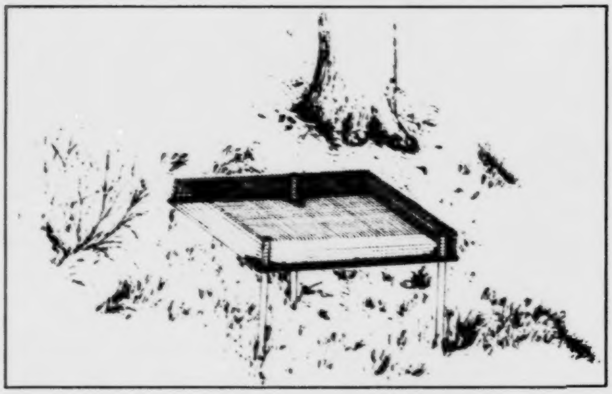

Figure 1. Sticky trap (18 × 24 in) for measuring early larval dispersal of the western spruce budworm in Montana.

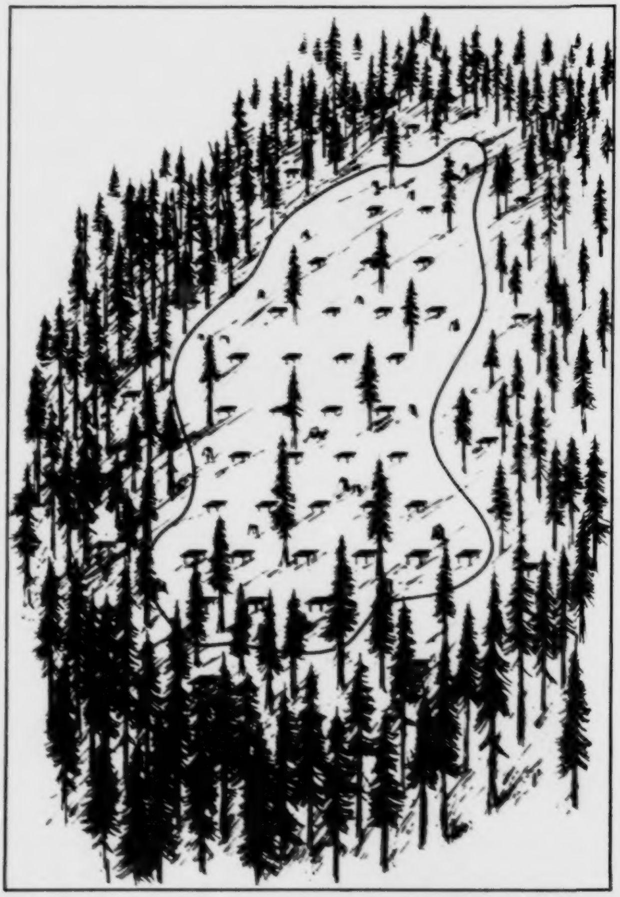

Figure 2. Grid system used for deploying larval dispersal traps.

than in clearcuts, apparently because the leave trees provide overwintering sites for larvae.

Another silvicultural treatment — removal or thinning of nonmerchantable "residue" understory trees — has a substantial effect on dispersing second instars. Significantly more larvae reach the ground where this understory is removed:

Forest	*Residue understory removed*		*Undisturbed forest*	
	Larvae/m²	*Larvae/ft²*	*Larvae/m²*	*Larvae/ft²*
A	*288*	*27*	*204*	*19*
B	*336*	*31*	*248*	*23*
C	*324*	*30*	*112*	*10*
D	*440*	*41*	*116*	*11*

We speculate that the impact of the budworm on regeneration will be less in those units where the understory residue remains standing.

To study adult dispersal related to silvicultural systems, we used either Pherocon II traps or half-gallon (2 L) modified milk carton traps mounted atop a 6-foot (2-m) pole and baited with 0.01 percent pheromone. Traps are placed in grid fashion in the cutting units — as shown for the larval dispersal traps (Figure 2).

In all silvicultural systems, regardless of the type or intensity of treatment, size of cutting unit or slope, aspect or population density, we consistently trapped significantly fewer moths in the treated area than in the adjacent undisturbed forest. Even in small 15-acre (6-ha) cutting units, we found — over a 2-year period — that the silvicultural system and the number of male moths trapped were closely related:

Treatment	*1978*	*1979*
	------ *(Moths per trap)*	------
Control	*12.3*	*15.7*
Understory removal	*12.1*	*11.3*
Overstory removal	*8.8*	*8.8*
Selection cut	*7.8*	*9.3*
Clearcut	*4.8*	*4.5*

The number of moths caught in the controls was not significantly different from those caught in the understory removal, the least severe silvicultural treatment. Significantly fewer moths were caught in the other three treatments, however.

Our results, supplemented by other data not presented here, are being integrated with data from a study on stand regeneration. Data from the two studies will be incorporated into the insect and stand dynamics model to develop a pest-management system for the western spruce budworm.

Springtime Behavior and Budworm Population Dynamics

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The behavioral patterns of spring-emerging second instars of western spruce budworm appear to be extremely critical, but remain largely unstudied. Recent studies[1,2,3] (Beckwith and Kemp 1984) have shown that the synchrony of host and insect phenology influences defoliation intensity. These studies strongly suggested that when adequate numbers of host shoots were sufficiently expanded, springtime budworm survival was greater than in years when the reverse was true.

The results of these studies imply that further discussions and work should be initiated on:

- Comparison of larval behavior in years when the host phenology precedes the insects and when conditions are reversed.
- Identification of the factors that cause a behavioral alternation from bud-mining to needle-mining (with its subsequent reduction in survival) by second instars in the early spring.
- Evaluation of the adaptative strategies of springtime needle-mining, passive airborne dispersal, and bud-mining.
- Quantification of differences in generation survival during years when initial springtime behavioral regimes are different (that is, needle-mining, bud-mining).

Literature Cited

Beckwith, R.C.; Kemp, W.P. 1984. Shoot growth models for Douglas-fir and grand fir. For. Sci. 30(3):743-746.

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[1] Dennis, B.; Kemp, W.P.; Beckwith, R.C. A stochastic model in insect phenology. I. Estimation and testing. (In preparation.)

[2] Kemp, W.P.; Beckwith, R.C. A comparison of phenology models developed for western spruce budworm host species in northeastern Oregon and north central Idaho. (In preparation.)

[3] Kemp, W.P.; Dennis, B.; Beckwith, R.C. A stochastic model of insect phenology. II. The western spruce budworm. (In preparation.)

Discussion Group A —
Budworm Behavior

Summary

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Behavior has a definite influence on the population dynamics of an insect species. Although we recognize many different aspects of insect behavior, we decided to discuss only dispersal and secondary diapause of budworm.

Adult dispersal results in both within-stand redistribution of the population and spread between stands, which may be either short or long range. Although adult dispersal is density dependent, the triggering mechanism is not thoroughly understood. Laboratory studies on the spruce budworm (*Choristoneura fumiferana* (Clemens)) showed greater female activity in pheromone-permeated air, but these results were not validated in the field. Fewer adults of western spruce budworm (*C. occidentalis* Freeman) were trapped in areas with silvicultural treatments (other than understory removal) than in undisturbed forests.

Silvicultural practices also affect larval dispersal. The survival of early larvae may closely depend on host synchrony. Clearcutting contributes substantially to dispersal losses of early instars. Understory removal allows more larvae to reach the forest floor, which may be detrimental to host regeneration. In open stands with little understory, about 25 percent of trapped second instars reach the forest floor and may be lost to the population; however, these early larval dispersal losses may be insignificant in terms of generation survival.

Second diapause is important in the population dynamics of *C. orae* Freeman and *C. biennis* Freeman and must be considered a normal part of their life cycles. Incidence of second diapause is low in *C. fumiferana* and *C. occidentalis*; however, it does occur naturally and may contribute to population survival and stability during periods of adverse weather.

Discussion Group A —
Host–Plant Interactions

Host Plant Nitrogen Dynamics and the Spruce Budworm

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The availability of nitrogen (N) can be limiting to the growth of plants and herbivores alike. The influence of nutrient supply on leaf assimilatory rate has been known since the turn of the century. Soil with an abundant supply of nutrients can produce, from the same quantity of foliage, twice the timber that can be produced on poor soil (Assman 1970). The richer sites tend to produce not only more efficient foliage with higher nutrient levels, but also more foliage per area.

The effect of nutrient supply on the performance of herbivores is not clear, but the best examples of foliar N limiting herbivore growth involve trees. This is probably because trees generally have lower N levels than herbaceous plants and tree N is thus more likely to be limiting to their herbivores. Spruce and fir foliar N is typically below 1.5 percent, which is unusually low, even for trees. Thus, it is not surprising that positive correlations between foliar N and budworm pupal weight have been found (Shaw et al. 1978; Mattson et al. 1983; Schmitt et al. 1983).

Because foliar N is a factor that determines the quality of spruce and fir foliage both in terms of tree growth and as insect food, any attempt to increase timber yield must be measured against change in susceptibility to budworm. The host/pest management problem is further exacerbated by the inclination of budworm hosts to allocate resources to maintain foliar nutrient levels (quality) at the expense of foliage mass (quantity). Mitscherlich's efficiency law (see Assman 1970) provides an explanation as to why this occurs. The law states that growth (increment increase) responds to changes in nutrient level in proportion to the difference between present and maximum growth rate, if other growth factors are kept constant. This means that once the concentration of a foliar nutrient is below a certain critical level, placing more of the nutrient in each unit of foliage will result in greater yield than if the nutrient is used to form more foliage with a lower concentration of the nutrient. Since spruce-fir foliar N is likely to be at an initial level much below that which yields maximum tree growth, any event such as defoliation that decreases the amount of N available for incorporation into foliage, will result in less foliage being produced rather than more foliage with a lower N concentration.

Figure 1 is a model that illustrates the effect of certain events on the allocation of a nutrient in limited supply. All events result in quality being maintained, in some cases at the expense of foliage quantity. Some events result in a change in size of the N pool with reallocation based on the efficiency law. Events such as budmining and weather reduce the number of needles and hence the N pool is divided between fewer needles. Some of the facts upon which the model is based are:

- Fertilization usually leads to an increase in both foliar N and foliar biomass (Assman 1970).
- The N supply is mostly dependent on previous years activities because 75 percent of the N that goes into expanding leaves comes from storage (Luxmore et al. 1981).
- The number of current-year needles is predetermined because conifer needle primordia are preformed.
- A cool, dry summer results in fewer primordia (Clements 1970) as does defoliation, which results in fewer needles with higher percentage N (Piene and Percy 1984).
- Destruction of buds by budworm mining reduces foliage but not N because foliage has not expanded.

The model indicates that a spruce-fir stand undergoing defoliation would maintain foliage quality and a vigorous budworm population until the supply of foliage is

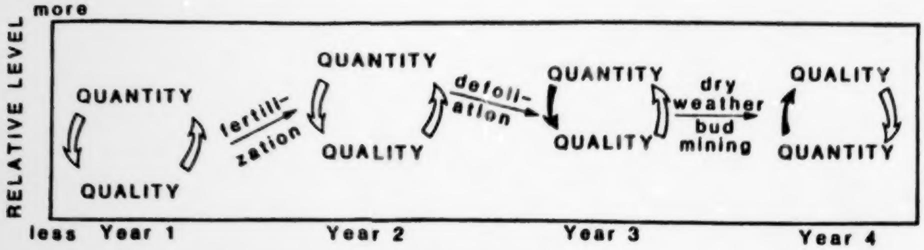

Figure 1. Idealization of nitrogen allocation between foliage quality and foliage quantity. External events can increase or decrease the nitrogen pool or leave the pool unchanged. These events then stimulate the internal mechanisms to shift the allocation equilibrium between quality and quantity.

depleted. This model does not take into account changes in secondary, defensive chemistry that may occur.

Literature Cited

Assman, E. 1970. The principles of forest yield study. Pergamon Press, Oxford. 506 pages.

Clements, J.R. 1970. Shoot responses of young red pine to watering applied over two seasons. Can. J. Bot. 48:75-80.

Luxmore, R.J.; Grizzard, T.; Strand, R.H. 1981. Nutrient translocation in the outer canopy and understory of an eastern deciduous forest. For. Sci. 27:505-518.

Mattson, W.J.; Slocum, S.S.; Koller, C.N. 1983. Spruce budworm (*Choristoneura fumiferana*) performance in relation to foliar chemistry of its host plants. Pages 55-65 *in* R.L. Talerico and M. Montgomery, eds. Proc. Forest defoliator-host interactions: A comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-85.

Piene, H.; Percy, K.E. 1984. Changes in needle morphology, anatomy, and mineral content during recovery of protected balsam fir trees initially defoliated by spruce budworm. Can. J. For. Res. 14:238-245.

Schmitt, M.D.C.; Czapowskyj, M.M.; Allen, D.C.; White, E.H.; Montgomery, M.E. 1983. Spruce budworm fecundity and foliar chemistry: Influence of site. Pages 97-103 *in* R.L. Talerico and M. Montgomery, eds. Proc. Forest defoliator-host interactions: A comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-85.

Shaw, G.G.; Little, C.H.A.; Durzan, D.J. 1978. Effect of fertilization of balsam fir trees on spruce budworm nutrition and development. Can. J. For. Res. 8:364-374.

Discussion Group A —
Host–Plant Interactions

Mechanism of Tree Resistance to Spruce Budworms — Is there a Terpene Connection?

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Eons of coevolution between plants and their herbivores have generated a multitude of strategies that plants use to defend themselves. Breeders can expose short-lived plant populations to pests and select survivors without understanding the mechanism of resistance. Through many generations, these resistant genotypes can be combined with other desirable traits and superior resistant selections developed. For long-lived species such as forest trees, this process requires much more time and is usually too costly. A more fruitful approach may be to determine the mechanisms for preferential host selection within or between trees and then search for genotypes that exhibit those resistant characteristics.

We discuss here potential mechanisms in forest trees that may be responsible for preferential selection by the two species of budworms and suggest which mechanisms are worthy of further evaluation.

Evidence for Natural Resistance to Western Spruce Budworm

As a result of coevolution, host plants of the western spruce budworm from an ecological perspective are well protected from severe impact. Budworm hosts have foliage available year round for many years continuously, but budworm feeding on this continuously available plant usually occurs only for a brief period during the life cycle of the tree and only during a brief period in the growing season. Therefore, western spruce budworm hosts have a truly small window of vulnerability (Figure 1), which might be further closed if responsible mechanisms were known.

Four host factors influence resistance against western spruce budworm: foliage age, phenology, physiological condition, and genotype. The insect exhibits a strong within-tree preference for certain foliage types. With the exception of needle mining by early instar larvae, it feeds almost exclusively on current year's foliage. Spruce budworm larvae forced to feed on second-year or older foliage had reduced survival (Heron 1964), reduced fecundity, and retarded development (Blais 1952, 1953). In the Southwest, budworms are only rarely observed feeding on second-year or older foliage, and when they do, feeding behavior is abnormal (M.R. Wagner, personal observation).

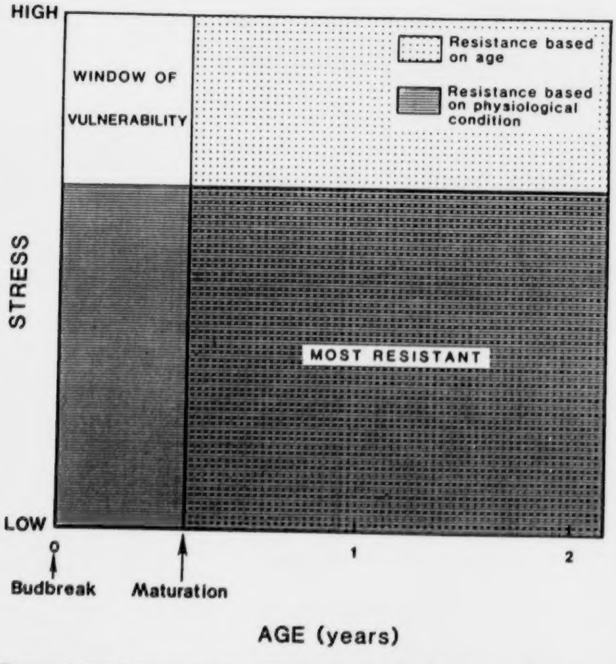

Figure 1. Window of vulnerability for budworm hosts created by host factors that confer resistance against feeding.

The quality of an insect's diet changes through the season (Scriber and Slanski 1981), and these seasonal changes in foliage quality may restrict spruce budworm feeding (Heron 1964). Feeding efficiency and growth rates of western spruce budworm larvae forced to feed on late season Douglas-fir and Engelmann spruce foliage were tremendously reduced (Blake 1983). There appears to be a foliage trait that changes through the season that makes the new foliage progressively less palatable to budworm.

Insect outbreaks tend to occur during periods of prolonged stress, which apparently reduces resistance of the plant and therefore increases the reproductive success of herbivores. Female adult weights of both western spruce budworm (Cates et al. 1983a) and spruce budworm (Mattson et al. 1983) were greater on artificially stressed trees. However, Blake (1983) found no difference in western spruce budworm performance on trees under high *vs.* low stress comparing within the range of naturally occurring stress.

Finally, McDonald (1981, 1982, 1983) has found genetically resistant genotypes of Douglas-fir. A genetic component influences budworm feeding, which is independent of foliage age, phenology, or stress.

Terpene Composition as a Potential Resistance Mechanism

Terpenes have been specifically implicated as factors influencing weight gain and adult weight in both species of budworm. Cates et al. (1983a) found the most important variables influencing budworm success were the concentration of several specific terpenes and changes in the distribution of foliar terpenes. Female western spruce budworm from trees high in foliar concentrations of beta-pinene and myrcene weighed less than those from trees with low concentrations (Redak and Cates 1984). Bornyl acetate and beta-pinene, when present in high concentrations in agar diets, reduced the dry weight of budworms (Cates et al. 1983b). Mattson et al. (1983) found several terpenes in both balsam fir and white spruce were negatively correlated with weight gain of *C. fumiferana*. Specific terpenes implicated by Mattson included: alpha-pinene, beta-pinene, camphene, beta-phellandrene, bornyl acetate, and terpinolene.

Terpene content is under strong genetic control (Hanover 1975). Species and geographic groups of *Abies* spp. and Douglas-fir, two important western spruce budworm hosts, can be identified based on variability in terpene composition (Zavarin and Snajberk 1973; Hunt and von Rudloff 1974).

When the terpene composition of resistant and susceptible foliage is compared, in almost every case, resistant foliage has higher amounts of certain terpenes than nonresistant. An interesting exception is citronellol and geranyl acetate. In at least one case, the resistant foliage has lower amounts of these terpenes. Mattson (personal communication) has suggested geranyl acetate is a feeding stimulant for spruce budworm. These analyses are confounded, however, by inability to separate geranyl acetate and citronellol.

Conclusions

Many potential mechanisms exist to explain preferential foliage and host selection by budworms. There are far too many possibilities to test them all. A more efficient approach would be to look for a common mechanism that confers resistance against budworm and creates the relatively small window of vulnerability. This will tend to find the most important and perhaps most useful mechanism, but not necessarily the only mechanism. Change in terpene composition meets many of the criteria for a good candidate mechanism of host plant resistance and deserves considerably more research.

Literature Cited

Blais, J.R. 1952. The relationship of the spruce budworm (*Choristoneura fumiferana* Clem.) to the flowering condition of balsam fir (*Abies balsamea*). Can. J. Zool. 30:1-29.

Blais, J.R. 1953. Effects of the destruction of the current year's foliage of balsam fir on the fecundity and habits of flight of the spruce budworm. Can. Entomol. 85:466-468.

Blake, E.A. 1983. Consumption rates and nutritional efficiencies of the western spruce budworm, *Choristoneura occidentalis* Freeman, in northern Arizona. M. Sc. thesis. Northern Arizona University, 88 p.

Cates, R.G.; Redak, R.A.; Henderson, C.B. 1983a. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions. Pages 3-20 *in* P. Hedin, ed. Mechanisms of plant resistance to insects. American Chemical Society Symposium Series 208, Washington, D.C. 375 p.

Cates, R.G.; Redak, R.; Henderson, C.B. 1983b. Natural product defensive chemistry of Douglas-fir, western spruce budworm success, and forest management practices. Zeitschrift fur Angewandte Entomologie 96(2):173-181.

Hanover, J.W. 1975. Physiology of tree resistance to insects. Annu. Rev. Entomol. 75-95.

Heron, R. 1964. The role of chemotactic stimuli in the feeding behavior of spruce budworm larvae on white spruce. Can. J. Zool. 43:247-269.

Hunt, R.S.; von Rudloff, E. 1974. Chemosystematic studies in the genus *Abies* I. Leaf and twig oil analysis of alpine and balsam firs. Can. J. Bot. 52:477-487.

Mattson, W.J.; Slocum, S.S.; Koller, C.N. 1983. Spruce budworm (*Choristoneura fumiferana*) performance in relation to foliar chemistry of its host plants. Pages 55-66 *in* Proc. CANUSA workshop, Forest defoliator–host interactions: A comparison between spruce budworm and gypsy moth. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Stn, Broomall, Pa. Gen. Tech. Rep. NE-85.

McDonald, G.I. 1981. Differential defoliation of neighboring Douglas-fir trees by western spruce budworm. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn, Ogden, UT., Res. Note INT-306. 10 p.

McDonald, G.I. 1982. Progeny testing of Douglas-fir seedlings for resistance to western spruce budworm. Pages 460-465 *in* Resistance to diseases and pests in forests trees. Pudoc, Wageningen.

McDonald, G.I. 1983. Douglas-fir progeny testing for resistance to western spruce budworm. Proc. CANUSA workshop, Forest defoliator–host interactions: A comparison between spruce budworm and gypsy moth. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Stn, Broomall, Pa. Gen. Tech. Rep. NE-85.

Redak, R.A.; Cates, R.G. 1984. Douglas-fir–spruce budworm interactions: The effect of nutrition, chemical defenses, tissue phenology, and tree physical parameters on budworm success. Oecologia. 62:61-67.

Scriber, J.M.; Slanski, F. 1981. The nutritional ecology of immature insects. Annu. Rev. Entomol. 26:183-221.

Zavarin, E.; Snajberk, K. 1973. Geographic variability of monoterpenes from cortex of *Pseudotsuga menziesii*. Pure and Appl. Chem. 34(3-4):401-410.

Discussion Group A —
Host–Plant Interactions

Role of Host Plants in the Population Dynamics of the Spruce Budworm

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Attempting to establish the role of host plants in the population dynamics of spruce budworms raises two critical questions at the outset.

First — are the host plants under any circumstances completely incompatible or immune to budworms? If so, their role is clear; host plants keep budworm numbers at or close to zero because the insects are incompatible with the plants. This may occur as the result of some special individual properties of plants or special population level properties such as certain stand structures, densities, or species mixes. On the other hand if there is no evidence of immunity (which is probably the case for most eastern host species except seedlings), then secondly — do the host plants have any mechanism for responding to and hence ultimately regulating changes in budworm density? For plants to serve in more than just a passive role as food and shelter, they need a mechanism that provides negative feedback to the regulating variables (survival, fertility, emigration and immigration) of the budworm population. Such mechanisms could reside both in the traits of individual plants and in the plant populations or the ecosystem to which individual plants belong. Many important plant traits (such as levels of nutrients, terpenes, and tannins) can vary and hence could serve to manipulate either the behavior or the physiology of the budworm, thereby bringing about negative feedback.

Hence, if the plants are not immune to budworms, in order to know if they have regulatory capacity, one needs to know if they have traits that respond in a density-dependent manner to budworm density and if such changes are powerful enough and in the direction of negative feedback.

Unfortunately our knowledge in this area is still primordial so that we cannot make any definitive pronouncements. Rather we can only speculate and raise significant hypotheses for further testing.

Let me offer a scenario that raises some significant questions. This is my perspective on the role of the true firs (namely balsam fir) in the population dynamics of the eastern budworm. White spruce is different and so are perhaps other hosts like red and black spruce in the east and Douglas-fir in the west. In the case of true firs, I speculate that during the early stages of ontogeny (seedling to sapling stage) most hosts have a near-immune trait profile. That is, young plants are only marginally compatible for budworms owing to high background levels of allelochemicals (such as terpenes) and an inducible defense system, both of which interact synergistically with natural enemies of budworms. Such plants rely on a high preformed defense system to reduce the performance level of those budworms who are the early colonizers.

For example, in balsam fir, young trees have about 40 percent more total terpenes than medium/mature trees. The result is that budworms grown on such trees are 10 to 20 percent smaller and less fecund. Moreover, owing to the feeding damage, plants may react in several ways, perhaps chemically, morphologically, and phenologically (all part of the inducible defense system) to deter further budworm expansion. Furthermore, activity of natural enemies may be enhanced by either visual, volatile or other cues offered by damaged plants, causing a synergistic interaction with inducible plant defenses. The net result is that mean budworm density remains low in such fir stands and fluctuations are quickly dampened owing to the inducible defense system and responsive natural enemies — e.g. pathogens, parasites, and predators. In this system we can visualize regulation of budworm. The crux of the issue is whether there is any kind of density-dependent defense system. This remains to be determined.

Later in the ontogeny of true firs, presumably as they have entered into full reproductive maturity, their preformed defense system declines and likewise so does their inducible system. Concomitantly, so do some tissue nutrient levels (sugars) which theoretically could reduce performance but do not because of compensatory feeding by insects. The net result is larger, more fecund insects which tend to lay most of their eggs in their mother stand rather than dispersing before ovipositing. Consequently, mean insect density is high and fluctuations run unchecked to the limits of food supply. The small negative feedback from chronic defoliation (e.g., less foliage) is not enough to limit budworm expansion before wholesale death occurs among the fir host population. In older stands, therefore, budworm population dynamics are not regulated by plants but by other factors. Plant stress owing to warm/dry weather may only exacerbate the problem by raising levels of some nutrients such as sugars and soluble N, and lowering terpenes, thereby improving budworm growth. From the plant's perspective the situation was out of control anyway because it no longer had any regulatory capacity. Host plants can only regulate the budworm if they have an inducible defense system. This system could be entirely within the plant, but more likely than not, it depends on synergistic interactions with natural enemies.

The scenario for true firs is apparently much different from that for other hosts because true firs are very likely to be killed during a budworm epidemic. Other hosts such as white, black, and Engelmann spruce and Douglas-fir are less likely to be killed because they have highly resistant or nearly immune old foliage which is seldom seriously depleted even during epidemics. Quite the opposite is true, for example, for balsam fir, where although its old foliage is less preferred and less nutritious, it is readily eaten by budworms. Hence, species other than true firs possess at the outset a level of immunity or near immunity because part of their foliage mass is safe from budworm. On top of this they may have adopted a strategy of tolerance for coping with budworms. In other words, they can tolerate and compensate for budworm feeding on new foliage because they have a large reserve mass of foliage with reserve photosynthetic capacity. The eastern spruces seem to protect their new foliage (<1 year-old) less than does balsam fir, maybe because it is less critical to their survival. White and black spruce, for example, have terpene levels that are only 20 percent and 66 percent, respectively, of those in balsam fir. It is also possible that these other hosts may have a powerful inducible defense.

Questions about the role of plants in the population dynamics of budworm inevitably lead to plant defenses or plant traits that are responsive to budworm density and that act in a density counteracting manner. If such traits don't exist, then plants will only serve passively in the dynamics of budworm — as food and shelter. Future research on plant resistance should seek to classify those traits which are responsive to budworm density and those which are not. These are important questions because they lead to an understanding about the origin of outbreaks and hence their cure.

Discussion Group A — Host–Plant Interactions

Potential Effects of Changes in Foliage Quality on Spruce Budworm (*Choristoneura fumiferana*) Population Dynamics

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It has long been known that stands of host trees differ in their likelihood of budworm damage and recently it has become apparent that many important nutritional parameters depend on stand maturity, tree species, needle age, and other factors affecting budworm growth, development, and potentially, density (e.g., Mattson et al. 1983). Hence questions arise whether certain stand characteristics could be manipulated to "favorably" alter budworm-forest dynamics. One such characteristic is foliage quality which measures the rate at which increases in foliage consumption per budworm are accompanied by increases in budworm reproductivity, all else being equal.

Anticipating the long-term consequences of reducing foliage quality requires an understanding of the cause and effect relationships underlying budworm-forest dynamics. Currently there is considerable disagreement regarding the relative importance of these relationships, largely as a result of different perspectives on the historical record of budworm outbreak patterns (Fleming 1985). For our purposes, however, the alternative theories of budworm-forest dynamics can be split into two groups. Most of the prevalent theories suggest that budworm reproductivity increases with stand age so that only in mature forests is reproductivity generally great enough for outbreak development. Outbreak collapse is thought to follow from a loss of food and egg laying sites resulting from defoliation and tree mortality. Reducing foliage quality has similar effects on the qualitative dynamics of the budworm-forest system in each of these theories: there is an immediate decline in the budworm's propensity for increase such that stands must generally be even older before outbreaks develop. But since stand vulnerability to budworm damage increases with stand age in these models, when outbreaks do occur, they are more destructive than they were before foliage quality was reduced. Thus, for these theories, reducing foliage quality extends the period between outbreaks but results in more forest damage when outbreaks occur.

Royama (1984) has developed a very different theory of budworm population dynamics: he concludes that a group of parasites, and perhaps density-dependent changes in the physiological vigor of individual budworms as well, "seem to be the only possible driving forces of [the periodic 30-40 year] budworm population oscillations." He favors a complex of viral and protozoan parasites, as yet poorly understood, and suggests the complex probably also includes diseases of a presently unknown nature. He implies that these parasite populations increase in response to concentrations of their budworm hosts so that outbreaks can be interrupted before forest damage becomes important. Since outbreak collapse deprives these parasites of their budworm hosts, parasite populations decline soon afterwards. A pattern of oscillations in parasite-budworm population densities typical of predator-prey relationships develops.

The effects of reducing foliage quality are less certain for Royama's theory than for those theories considered earlier. The lack of data and vagueness of his theory, especially regarding the nature and attributes of the proposed regulating agents, make prediction difficult. Nonetheless, despite these reservations, the slower rise of budworm populations to outbreak levels caused by poorer foliage quality could produce longer intervals between outbreaks and more severe outbreaks in the short-term (Fleming 1983; Régnière 1984). The long-term offers a wider range of possibilities, from continuation of the same short-term outbreak pattern to the development of much less desirable ones. As an example of the latter, Anderson and May (1981) demonstrate that parasites lacking alternate hosts may not persist if their principal hosts maintain low densities for long periods. Thus budworm might escape such parasites during the more extended intervals between outbreaks caused by foliage quality decreases and become an even more damaging pest than it had been before.

In summary, the prevalent theories of budworm population dynamics predict similar immediate consequences for foliage quality reductions: increased outbreak severity and decreased outbreak frequency. Forest managers might benefit from the reduced frequency in two ways: first, a stand need be cut less often to preclude severe budworm damage so the relative economic costs of harvesting affected stands should decline; second, forests could accumulate greater wood volumes between outbreaks so stand values at cutting time should increase. The long-term implications of these theories are less easily established; it should not be unequivocally assumed that reducing foliage quality will necessarily "improve" the budworm problem.

Literature Cited

Anderson, R.M.; May, R.M. 1981. The population dynamics of microparasites and their invertebrate hosts. Phil. Trans. Roy. Soc. (Lond.) 291:451-524.

Fleming, R.A. 1983. Foliage quality and its effect on budworm populations: a modeller's viewpoint. Pages 113-123 *in* Proc. Forest defoliator–host interactions: A comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., N.E. For. Exp. Stn., Broomall, PA. Gen. Tech. Rep. NE-85.

Fleming, R.A. 1985. How should one view the historical record of spruce budworm outbreaks? Pages 136-137 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Mattson, W.J.; Slocum, S.S.; Koller, C.N. 1983. Spruce budworm (*Choristoneura fumiferana*) performance in relation to foliar chemistry of its host plants. Pages 55-56 *in* Proc. Forest defoliator–host interactions: A comparison between gypsy moth and spruce budworms. U.S. Dept. Agric., For. Serv., N.E. For. Exp. Stn., Broomall, PA. Gen. Tech. Rep. NE-85.

Régnière, J. 1984. Vertical transmission of diseases and population dynamics of insects with discrete generations: A model. J. Theor. Biol. 107:287-301.

Royama, T. 1984. Population dynamics of the spruce budworm, *Choristoneura fumiferana* (Clem.): A reinterpretation of life table studies from the Green River project. Ecol. Monog. 54(4):429-462.

Discussion Group A —
Host–Plant Interactions

The Effect of Chemical Defenses, Nutrition, Needle Phenology, and Physical Parameters of Douglas-fir on Western Spruce Budworm Success

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The overall objective of several different types of investigations was to determine the effect of secondary chemistry, nitrogen content, phenology of the current year's needles, and physical parameters of Douglas-fir trees on western spruce budworm larval growth, survival and adult dry weight production. The knowledge gained from such studies would contribute important information to the areas of host resistance, plant and herbivore population biology, the effects of predators and parasitoids on herbivores, and to the silviculture management of forest systems (Wulf and Cates, in press).

The location of the sites in Montana and New Mexico, and detailed procedures, methods, and statistical approaches are found in Redak and Cates (1984), Cates et al. (1983a,b), and Cates et al., (in press [a,b]). The study at the Montana site involved trees that were naturally infested with moderate levels of budworm. At the New Mexico sites budworm were placed on trees that were experiencing low levels of budworm. However, the Jemez study was designed as a water stress experiment involving trenched trees on a south facing slope that were compared to nontrenched trees on a north facing slope.

Data from all field studies show that the terpene chemistry of young foliage was the most important factor in reducing budworm success (Table 1).

Protein complexing capacity did not enter into any of the models or analyses, while nitrogen content was always a minor component except for a strong inverse relationship with female dry weight at the Barley Canyon site. The behavior of nitrogen in the Barley Canyon model suggested that it functioned more as an indicator of tree vigor than as a toxic agent. Tree age was almost always associated with susceptibility while budbreak and several indicators of vigor were inversely associated with budworm success.

Table 1
A summary of the relationship between Douglas-fir foliage quality and physical tree variables to western spruce budworm success

	Montana	*Barley Canyon, New Mexico*		*Jemez Springs, New Mexico*
Variables		*Female*	*Male*	
Foliage quality:				
% Nitrogen	*Weak positive*	*Strong inverse*	*Weak positive*	*Weak positive*
Terpenes[1]	*Acetate fraction* *Terpene distribution* *Myrcene* *Terpene 10*	*Terpene 5* *β-pinene* *Myrcene*	*Terpinolene* *Citronellyl acetate* *α-pinene* *Bornyl acetate* *Myrcene* *Terpene 8* *Terpene 5*	*Bornyl acetate* *β-pinene*
Protein complexing capacity[2]	*No*	*No*	*No*	*No*
Physical factors:				
Positive relationship	*Tree age*	*Tree age* *Internode length*	*Tissue water content* *Internode length*	*Tree age*
Inverse relationship	*Budbreak* *Bole radius*	*5-year growth increment*	*Crown ratio*	*None*

[1] Terpenes shown to have inverse relationships with budworm success variables measured in field studies on 3 different populations of Douglas-fir.

[2] No relationship detected.

These data support some of the contentions of current plant-herbivore theory but also provide several new insights. The importance of tissue quality in budworm success is clearly established, thereby providing the basis for suggesting that silviculture manipulations may be effective against the budworm. The data further suggest a strong link between biotic and abiotic factors that lead to host stress changes in defensive chemistry and nutrition, and eventually to outbreaks of budworm (Wulf and Cates, in press). But these and other data not presented here also suggest that much more information is needed to determine the ramifications of geographic variation in host resistance in Douglas-fir, and other hosts, the response of budworm to this variation, and the importance of foliage quality in budworm population dynamics as compared to other biotic agents.

Literature Cited

Cates, R.G.; Redak, R.; Henderson, C. 1983a. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions. Pages 1-19 *in* P.A. Hedin, ed. Plant Resistance to Insects. Amer. Chem. Soc. Symp. Series 208. Washington, D.C.

Cates, R.G.; Redak, R.; Henderson, C. 1983b. Natural product defensive chemistry of Douglas-fir, western spruce budworm success, and forest management practices. Z. Angew, Entomol. 96:173-182.

Cates, R.G.; Redak, R.; Henderson, C.; McMurray, T. (In press [a]). Stress physiology, patterns in defensive chemistry, and spruce budworm success. Z. Angew. Entomol. (submitted).

Cates, R.G.; Henderson, C.; Redak, R. (In press [b]). Responses of western spruce budworm to varying levels of nitrogen and terpenes. Oecologia (submitted).

Redak, R.; Cates, R.G. 1984. Douglas-fir (*Pseudotsuga menziesii*) – spruce budworm (*Choristoneura occidentalis*) interactions: the effect of nutrition, chemical defenses, tissue phenology, and tree physical parameters on budworm success. Oecologia 62:61-67.

Wulf, N.W.; Cates, R.G. (in press). Site and stand characteristics. *In* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech. coords. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1694.

Discussion Group A —
Host–Plant Interactions

Summary

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Research on the effects of host plants in the population dynamics of spruce budworm has been addressed from two points of view: 1) effects of properties of individual trees and 2) effects of properties of populations of trees, i.e., forest stands. To develop a holistic understanding of the role of host plants in budworm epidemiology, research progress in both areas is essential.

The panel discussion centered mainly on individual tree effects because the majority of panelists researched this area. The consensus is that most host plants are suboptimal for budworm performance (survival and growth) owing to less than optimal levels of basic nutrients, particularly protein and metabolizable carbohydrates, and higher than optimal levels of nonnutrients such as tannins and terpenes. Plant stress is positively correlated with increasing budworm performance, particularly higher weight gains, and thus fecundity, because it apparently increases levels of nutrients. Likewise, moderate fertilization usually brings about improved budworm weight gains for the same reasons — particularly elevated N levels.

The most nutrient-rich plant tissue is current foliage. Hence, when budworm populations increase to the point where they are forced through competition to feed on older (≥ 1 year-old) foliage, their overall performance will substantially decline. Such foliage is not only more nutrient-poor but also more fibrous and thus more difficult from which to extract scarce nutrients. In the case of spruces and Douglas-fir, there may be additional factors such as feeding deterrents and/or lowered levels of feeding stimulants in older foliage, thereby making it almost unacceptable to even starving budworms. On the other hand, older foliage of true firs is more acceptable to budworms and will be eaten readily when new foliage is depleted.

Research accomplished under the auspices of the CANUSA Program has made a significant inroad into the chasm of ignorance about host plant effects on budworm outbreaks. However, there is much still to be learned, especially about differences between young versus older trees and whether the hosts have inducible defense systems that are triggered in response to budworm feeding. Even more importantly, it is essential to learn if the host plant defenses increase in relationship to budworm population density, i.e., whether the defenses are density-dependent. Answers to these questions will help elucidate the role of host plants in regulating budworm populations. Finally, there is a need to extensively screen host plants for significant variations in their susceptibility/resistance to budworm. This information might be useful in future tree improvement programs.

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Interpreting the Environment of Western Budworm Outbreak-Prone Site-Stand Configurations

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Models relating the amount of defoliation in an outbreak to descriptive site and stand characteristics portray budworm population responses to a variety of habitat conditions. Stands with heavy defoliation may be viewed as habitats suitable for the insects' population increase. By evaluating the models, one may define environmental characteristics conducive to outbreaks and conceptualize the interactions between the insect and the forest. Here we illustrate this, using empirical models we developed in Idaho to predict defoliation by the western spruce budworm (*Choristoneura occidentalis* Freeman).[1]

Hazard models were developed for western spruce budworm outbreaks on the Clearwater and Salmon National Forests during the late 1970s. Models differed with vegetation series. For host stands within the cool, high elevation subalpine fir series of north-central Idaho, defoliation increased with decreasing elevation, and with increasing stand density and amount of woody residue on the forest floor. Opposite relationships were found on the warm-moist western hemlock series occupying low to mid-elevation zones. In both series defoliation was inversely related to average stand age and deviation in tree age. Highest defoliation occurred in an elevation zone centered at about 1500 m (4,922 ft). Other analyses indicated that defoliations are heavier in host stands in the seral stage of succession, in stands on southwesterly aspects, on ridge tops and upper slopes, on grand fir and subalpine fir habitat types, and in western spruce budworm host-dominated stands. True fir sustained heavier defoliation than Douglas-fir or Engelmann spruce. In the Douglas-fir series of south-central Idaho high risk stands were of low density, without a duff layer and dominated by Douglas-fir with good but declining radial increments. Heaviest defoliations occurred at about 1800 m (5,900 ft) elevation.

Interpreting the Models

Results indicate that condition of the site and the dynamics of the insect are linked. One possible link is host foliage quality. The biochemical composition of the foliage, known to affect larval survival and adult fecundity, is determined by the physiological condition of the host tree. The latter reflects the tree's response to conditions of its growing site. Thus, site and stand characteristics may influence defoliator populations by affecting metabolism, synthesis, and concentration of host foliage compounds. This inference allows a consistent interpretation of the various defoliation trends shown in the empirical models.

Based on the relationships among variables of budworm hazard models, we derived the following inferences:

Vegetation Series. Model differences among vegetation series reflect climatic differences and the effects of those climates on soil forming processes (especially organic matter decomposition rates) and floristic composition, growth, developmental dynamics, and history of the forest and its fauna.

High risk – Elevation Zone. Budworm defoliation levels were highest within a certain elevation zone and decreased at elevations above or below that zone. This relationship may reflect 1) changes in host tree predisposition to budworm herbivory associated with altitude-related changes in soil pH and cation-exchange capacity, 2) impaired budworm survival under harsh high-altitude conditions, and 3) synchronization of host-tree and budworm developmental state, i.e., budburst and larval eclosion.

Average Stand Age and Deviation of Age. Stand age and variation in age indicate the successional phase of stand development and, consequently, a certain range of environmental conditions.

Tree age characteristics of high budworm risk stands in the western hemlock and subalpine fir series are typical of stands in the seral aggradation phase (*sensu* Borman and Likens 1978). This phase is characterized by high demands for "balanced" nutrition and low soil levels of decomposed organic matter. Such conditions are apt to cause nutritional stress, particuarly in species adapted to climax conditions (i.e. *Abies* spp.). Similar conditions characterize stands in the seral culmination phase where tie-up of nutrients in accumulated phytomass acerbates the situation.

Decreasing defoliation on the western hemlock and the subalpine fir vegetation series was associated with increasing average stand age and deviation of age, conditions descriptive of stands in the subclimax aggradation phase and the climax stage of succession. Forests in these developmental stages feature an abundance of decomposed organic matter, high levels of mycorrhizal activity and a relatively high ammonia nitrogen content in the soil solution. Increased nutrient availability, combined with possible lower nutrient demand, should reduce the chance of tree nutrient stress and, consequently, of predisposition of host trees to budworm herbivory.

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[1] Stoszek, K.J., and P.G. Mika. 1983. The relationships of western spruce budworm outbreaks to site-stand attributes, development and management history: Model completion and comparison. College of FWR, Univ. of Idaho, Moscow, ID; CANUSA-West Budworm Program, Final Report. 70 p.

[2] Nalley, R.N. 1982. Relationships of dead downed woody fuels to site and stand characteristics within the *Thuja plicata/Pachistima myrsinites* habitat type of northern Idaho. M.S. thesis, Univ. of Idaho, Moscow. 86 p.

Stand Density. Indices of stand density reflect microsite modification of climate. By altering temperature and light regimes and air flow patterns within the stand, density can influence decomposition, nutrient availability and uptake. The positive correlation of budworm defoliation to stand density on the cool subalpine fir series suggests that, in the stand, shading decreases air and soil temperatures and, consequently, mineralization rates and nutrient uptake. The opposite correlation found on the warm and moist western hemlock series seems to reflect a decrease in mineralization rates and nutrient availability brought about by increased insolation and ambient temperature and decreased soil moisture. Combined with high demands of fast growing trees for balanced nutrition, these conditions may result in tree nutrient stress. *Abies* spp., physiologically ill-adapted to environmental conditions of the seral stage of succession, may be particularly prone to such stress.

Amount of Woody Residue and Duff. The amount of residue on the forest floor is a function of stand successional development, composition, structure, use history, and site productivity.[2] Conditional on the climatic regime and fire history of the site, residue levels reflect decomposition rates and availability of mineral nutrients.

On the cool subalpine fir series defoliation was positively correlated with amount of woody residue. Given the acidic, poorly developed soils of this series, high residue levels indicate low decomposition rates, tie-up of nutrients and depletion of the soil's available nutrients.

On the warm-moist western hemlock series the correlation of budworm defoliation to amount of woody residues was negative. Due to generally well-developed soils and excellent mineralization rates, high residue levels on such sites are not indicative of nutrient availability problems. Low residue levels, particularly in seral stands, suggest that an intensive fire destroyed existing residue before development of the present stand. This loss could disrupt the nutrient transfer chain (Harvey et al. 1981) and discouple the ion cycle (*sensu* Ulrich 1982), and cause nutrient stress in host trees. Similarly, in Douglas-fir stands on the warm-dry Douglas-fir series low mineralization rates and a history of frequent ground fires leads to possible reduction of the soil's cation-exchange capacity and frequent discoupling of the ion cycle.

Thus, budworm outbreaks are seen as symptoms of a forest system under nutritional stress, and of host trees with foliage quality conducive to budworm population increases. Even though the population release mechanism remains unidentified, we suggest that nutrient stress is a key factor in the predisposition of host trees to herbivory.

Literature Cited

Borman, F.H.; Likens, G.E. 1979. Pattern and process in a forested ecosystem. Springer Verlag, New York.

Harvey, A.E.; Larsen, A.J.; Jurgensen, J.F. 1981. Rate of woody residue incorporation within northern Rocky Mountain forest soils. U.S. Dep. Agric., For. Serv., For. Res. Exp. Stn., Ogden, UT. Res. Pap. INT-282. 5 p.

Ulrich, B. 1982. A concept of forest ecosystem stability and acid deposition as a driving force of destabilization. Pages 1-29 *In* Ulrich and Pankrath, eds., Effects of accumulation of air pollutants in forest ecosystems. D. Reidel Publ. Co., Boston. 389 p.

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Historical Western Spruce Budworm Outbreak Frequency

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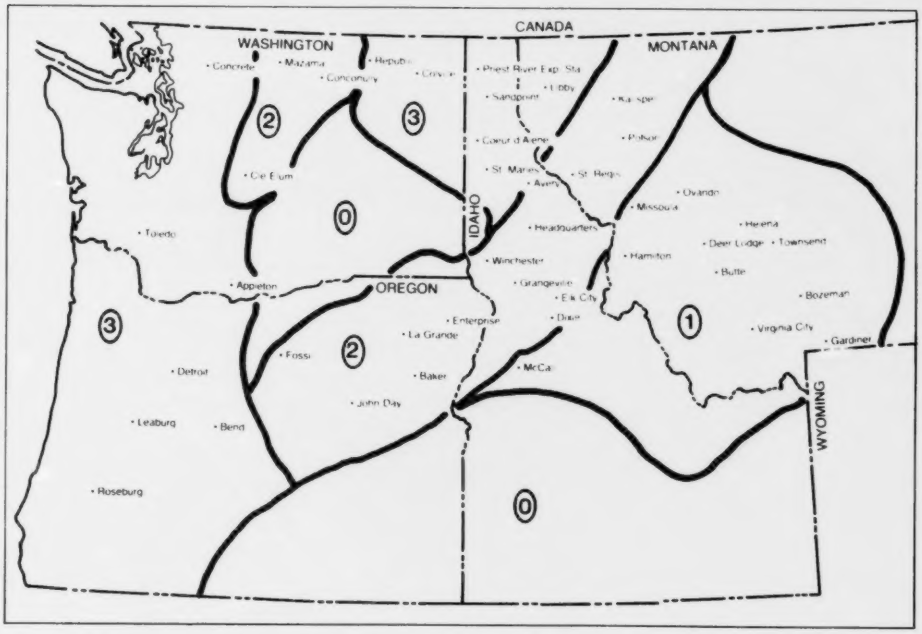
A cursory examination of historical defoliation records reveals that the western spruce budworm (*Choristoneura occidentalis* Freeman) reaches outbreak densities (causing visible defoliation) in only certain parts of its overall range.

To identify reasons for historically variable western spruce budworm defoliation, Kemp (1983), Kemp and Moody (1984) and Kemp et al. (1985) conducted studies to determine possible relationships between historical western spruce budworm defoliation records, historical climate records, and soil conditions.

Forty-three locations distributed as evenly as possible throughout Idaho, Montana, Oregon, and Washington, subject to the proximity of proper forest types and completeness of western spruce budworm defoliation data (1948-1978), were selected for analyses (Figure 1). At each location, a "zone of influence" was established to assess annual defoliation (1948-1978) patterns. This consisted of the area within a 20.92 km (13 mi.) radius of each selected location. This procedure provided a standardized assessment of budworm defoliation (>20 percent of current foliage) around each location each year.

If any area within the zone of influence of a location in a given year had defoliation recorded, it was considered an outbreak year (i.e., was recorded 0 = no defoliation or 1 = defoliation). A defoliation index value was then developed for each location by dividing the number of years when defoliation occurred in the zone of influence by the total number of years when defoliation was measured. The defoliation index values, which ranged from 0.0 to 1.0, were used to classify forested areas of the states in Figure 1. Locations in outbreak region 1 (high outbreak frequency) had index values between 0.60 and 1.00; areas classified as 2 or medium outbreak frequency, had values between 0.07 and 0.48; and areas classified as 3 or low outbreak frequency, had index values between 0.00 and 0.11 (Figure 1).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Sandpoint
Kalispell
Coeur d'Alene
Polson
Cle Elum
St. Maries
Avery
St. Regis
Ovando
Missoula
Toledo
Headquarters
Helena
Deer Lodge
Townsend
Hamilton
Winchester
Butte
Appleton
Grangeville
Elk City
Bozeman
Enterprise
Dixie
La Grande
Virginia City
Gardiner
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Figure 1. Map showing three classes of western spruce budworm outbreak frequency (1947-1978) developed for the forested areas of Idaho, Montana, Oregon and Washington (high outbreak frequency = 1, medium outbreak frequency = 2, low outbreak frequency = 3 (from Kemp, 1983).

To evaluate the general range of climates associated with the three outbreak frequency classes, a series of acetate map overlays were used with a base map of the four states of interest (Figure 1). Next, 335 points were selected from a grid representing a systematic sample across the four states, and data were collected on historical mean maximum and minimum temperatures and annual precipitation. Statistical comparisons based on the five climatic variables showed that the climate in areas with a history of frequent western spruce budworm outbreaks is characterized by low annual precipitation, low mean maximum temperatures for the month of January, and low July mean minimum temperatures (Figure 1). The climate in areas of low western spruce budworm outbreak frequency was characterized by higher temperatures and greater precipitation annually.

A transect of 80 sample points across north Idaho and western Montana was established for the collection of soil data in regions where historical western spruce budworm outbreak frequency ranged from low (north Idaho) to high (western Montana) (Figure 1). A wide range of soils and host foliage samples were collected for minerological analysis. Field and laboratory data on soil and foliage characteristics by outbreak frequency class (Figure 1) showed several significant differences. Soils from areas with high western spruce budworm outbreak frequency had no volcanic ash, low available moisture and low extractable aluminum compared to other outbreak frequency classes. Current year budworm host foliage from areas with high outbreak frequency had high sodium and phosphorous levels and low calcium.

Results suggest strong relationships between western spruce budworm outbreak frequency and fall and spring temperature regimes. This could occur through several pathways. Milder winter climates may result in the accumulation of fewer than the required number of chilling hours or degree days for successful spring emergence. Further, highly variable temperatures during the winter may initiate larval development too early due to a warming trend and result in increased mortality when temperatures fall below a critical level. Lastly, milder winter temperatures may disrupt host plant/insect synchrony in the spring and result in greater larval mortality.

As noted above, mean annual precipitation increases were also associated with a reduction in spruce budworm outbreak frequency. This again suggests the possibility of several relationships. First, host species in drier climates may be more prone to drought stress and thus these areas will likely exhibit higher outbreak frequencies. Direct effects of increasing precipitation on the western spruce budworm at whatever stage may limit survival in a variety of ways and thus limit outbreak frequency.

Results also suggest that on the average, host trees growing in areas with significant volcanic ash deposits may have fewer problems with available moisture. The coincidence of high outbreak frequency, low precipitation, and low amounts of weathered volcanic ash in high outbreak frequency class of Figure 1 suggests a strong relationship between host plant stress and western spruce budworm outbreaks.

Literature Cited

Kemp, W.P. 1983. The influence of climate, phenology and soils on western spruce budworm defoliation. Ph.D. dissertation. University of Idaho, Moscow, Idaho. 143 p.

Kemp, W.P.; Moody, U.L. 1984. Relationships between regional soils and foliage characteristics and western spruce budworm (Lepidoptera: Tortricidae) outbreak frequency. Environ. Entomol. 13: 1291-1297.

Kemp. W.P.; Everson, D.O.; Wellington, W.G. 1985. Relationships between regional climatic patterns and western spruce budworm outbreak frequency. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1693.

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The Spruce Budworm and the Forest

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Outbreaks of the spruce budworm (*Choristoneura fumiferana* (Clem.)) are a natural phenomenon, the result of the coevolution of a plant-insect system. If this premise is true it is inevitable that an interrelationship exists between the insect and the forest. The history of outbreaks has been determined for periods of 200 to 300 years for most regions affected by this insect (Blais 1983). These records reveal that outbreaks have occurred more frequently in the 20th century than previously. In recent times the interval between outbreaks within a region has varied between 19 and 37 years; prior to the 20th century intervals of 60 to 100 years were common. Earlier infestations were restricted to specific regions, but in the 20th century they have coalesced and increased in size. Reasons for the increase in the frequency and extent of infestations are mostly attributable to changes caused by man in the forest ecosystem. Clearcutting of pulpwood stands, fire protection, and use of pesticides against budworm favor the presence of balsam fir, the preferred host of the insect.

The most important prerequisite to infestations appears to be the presence of mature balsam fir over extensive areas. This does not mean that spruce-fir stands must be continuous. Over much of the area prone to budworm attack, fir occurs in mixed stands or in more or less isolated pure stands. It is significant that severe and prolonged outbreaks have recurred in western Ontario where fir comprises only 1 to 10 percent of the forest, much less than in regions further east (Halliday and Brown 1943) (Figure 1). This would suggest that the presence of fir is not necessarily a prerequisite to infestations. However, a closer look at the situation in western Ontario points to the contrary. In this region, there are two small sectors where fir comprises between 11 and 30 percent of the forest, one along the southwest shore of Lake Nipigon, the other near Sioux Lookout (Figure 1). It is precisely in these two sectors that several outbreaks began: in the Lake Nipigon sector in 1880, 1940, and 1980, and in the Sioux Lookout sector in 1862 and 1940 (Blais 1959; Elliott 1960; House et al. 1982).

Except in a few regions where climate is marginal for the insect, uncontrolled outbreaks have come to an end as a result of food depletion. Outbreaks do not change forest composition but are associated with fluctuations in the volume of fir and, to a lesser degree, of spruce.

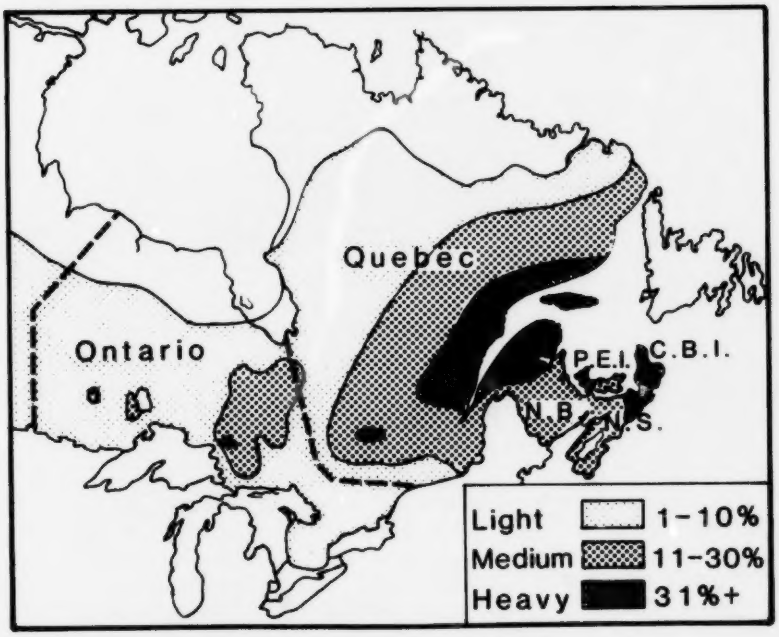

Figure 1. Map showing population intensity of balsam fir in eastern Canada according to Halliday and Brown (1943).

Records show that outbreaks can originate in both the Boreal Forest Region and the Great Lake-St. Lawrence Forest Region (Blais 1959; Elliott 1960; House et al. 1981, 1982; Hardy et al. 1983). A better understanding of the insect forest relationship based on the behavior of various outbreaks in several regions is required before forest management methods aimed at reducing the susceptibility and vulnerability of the forest to budworm attack can be put into practice.

Literature Cited

Blais, J.R. 1959. The recurrence of spruce budworm infestations in the past century in the Lac Seul area of northwestern Ontario. Ecology 35: 62-71.

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13: 539-547.

Elliott, K.R. 1960. A history of recent infestations of the spruce budworm in northwestern Ontario, and an estimate of resultant timber losses. For. Chron. 36: 61-82.

Halliday, W.E.D.; Brown, A.W.A. 1943. The distribution pattern of some important trees in Canada. Ecology 24: 353-373.

Hardy, Y.J.; Lafond, A.; Hamel, A. 1983. Epidemiology of the current spruce budworm outbreak in Quebec. For. Sci. 29: 715-725.

House, G.W.; Gross, H.L.; Rose, A.H. 1981. Pages 51-69 *In* Annual Report, Forest Insect and Disease Survey 1977. Can. For. Serv., Ottawa, Ont.

House, G.W.; Harnden, A.A.; Meating, J.H.; Carrow, J.R. 1982. The 1980 spruce budworm situation in Ontario. Can. For. Serv., Greak Lakes For. Res. Centre, Sault Ste. Marie, Ont. Inf. Rep. O-X-343. 92 p.

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How should one view the Historical Record of Spruce Budworm Outbreaks?

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The historical record of outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) comprises three principal sources: 1) radial growth patterns in old host trees which imprecisely take the record back to 1710; 2) intensive budworm censuses taken in the Green River area, 1947-1958; and 3) regional surveys conducted annually since 1947 to measure the budworm threat. Different perspectives on this record have led to disagreement about the causes of budworm population fluctuations.

The tree ring data suggest that spruce budworm densities have long followed the same basic oscillatory cycle, and the Green River data indicate that the local population trends were largely caused by changes in large larval survival. Royama (1984) proposes a single universal cause which could determine these trends and shows how his proposal is consistent with certain large-scale patterns of outbreak spread and collapse. But Royama's extrapolation of his analysis of 12 years of data from the Green River to 250 years of tree ring data and 30 years of province-wide survey data rests critically on an assumption of homogeneity in time. This is essentially an assumption that the intensities of factors affecting regional budworm population dynamics have been repeating the same temporal pattern over and over. The perceived validity of this assumption hinges on how one sees budworm-forest interaction. If one views the budworm as a relatively independent component of its ecosystem, the lack of overall temporal trends in budworm densities (Royama 1984, Fig. 3) lend support to the assumption. But if one considers the budworm as one of many mutually interdependent components of the forest ecosystem, trends underlying the fluctuations of other potentially important factors (cf. Blais 1983) leave this assumption questionable.

The large-scale, budworm-forest simulation models represent another approach to the historical record. Synthesizing Green River results, Holling (1978) and Stedinger (1977) model key ecological processes (e.g., growth, reproduction) driving budworm-forest dynamics and test their models by subjectively comparing outbreak patterns in the historical record with corresponding model output. Although large-scale simulation may eventually allow the most thorough synthesis and testing of our understanding, questions exist for these particular models about the way the Green River data are used and about the robustness of the testing (Royama 1984; Stedinger 1977).

Other researchers limit their analyses to regional survey data and infer explanations for their results from current understanding of the underlying ecological processes. Sippell (1984) subjectively analyzes the 1947-1983 maps of Ontario budworm densities and essentially repeats Stedinger's hypothesis for population fluctuations. Fleming et al. (1983, 1984) quantitatively analyze Maine's 1975-1980 survey data, considering forest condition as well as budworm densities and assessing the impact of large-scale spraying operations. Such analyses of regional survey data provide unique perspectives on budworm-forest dynamics but suffer from short-comings in survey methodology.

Ultimately, comprehensive theories of budworm dynamics must satisfactorily explain all the historical record. But only sound basic research can distinguish cause from correlation, and lack of such research leaves us short on understanding. Under these circumstances, no single "right way" of viewing the historical record is presently identifiable; each view deserves consideration but with full recognition of its potential shortcomings, particularly by its proponents.

Literature Cited

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13:539-547.

Fleming, R.A.; Shoemaker, C.A.; Stedinger, J.R. 1983. Analysis of the regional dynamics of unsprayed spruce budworm (Lepidoptera: Tortricidae) populations. Environ. Entomol. 12:707-713.

Fleming, R.A.; Shoemaker, C.A.; Stedinger, J.R. 1984. An assessment of the impact of large-scale spraying operations on the regional dynamics of spruce budworm, (Lepidoptera: Tortricidae), populations. Can. Entomol. 116:633-644.

Holling, C.S. (ed.) 1978. Adaptive Environmental Assessment and Management, John Wiley and Sons, London, U.K., 377 p.

Royama, T. 1984. Population dynamics of the spruce budworm, *Choristoneura fumiferana* (Clem.): A reinterpretation of life table studies from the Green River Project. Ecol. Monogr. 54(4): 429-462.

Sippell, W.L. 1984. Planning now to reduce, postpone or prevent the next spruce budworm outbreak. Pages 59-67 *in* Proc. New and improved techniques for monitoring and evaluating spruce budworm populations. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Stn., Broomall, PA. Gen, Tech. Rep. NE-88.

Stedinger, J.R. 1977. Spruce budworm management models. Ph.D. dissertation, Harvard University, Cambridge, MA. 260 p.

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The Historical Record and its Value in Developing Chronologies for Western Spruce Budworms

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Only short-term records of population density fluctuations of western spruce budworms have been compiled to date. Analyses which depend on extended longitudinal records are therefore impossible. Analyses of records compiled from data collected in several locations for short periods are unlikely to be helpful in illuminating long-term population behavior. Consequently, other sources of data, such as population indexes (*sensu* Morris 1955), must be sought.

In the Pacific states, the earliest record of what became known as the western spruce budworm (*Choristoneura occidentalis* Freeman) is a 1914 rearing from Douglas-fir at Ashland, Oregon (Lindsten et al. 1949, quoted by Dolph 1980). Minor outbreaks were recorded in 1929 and 1931, but it was not until 1943 that large-scale outbreaks were first recorded (Dolph 1980). An exhaustive listing of observations and summaries of defoliation caused by western spruce budworm from 1922 to 1971 in the northern Rocky Mountain states has also been compiled (Johnson and Denton 1975). Detailed defoliation maps of this area have been compiled since 1948. Together these records cover at least two widespread outbreaks of the western spruce budworm and the modoc budworm (*Choristoneura retiniana* Walsingham). Although these records do not provide an exact record of population change, this information may be used to estimate parameters associated with outbreak characteristics in a region (Kemp 1983).

Defoliation records also form the basis for calibrating tree ring records to generate proxy data on population fluctuations of the two budworm species in the United States. Defoliation signatures have been described for western spruce budworm in growth rings of its three principal hosts (Williams 1967), for volume losses on grand fir (Ferrell and Scharpf 1982) in the Intermountain region, and for modoc budworm on white fir (Ferrell 1980). Swetnam is also working on defoliation signatures in northern New Mexico. Before regional budworm chronologies can by synthesized, however, techniques to distinguish budworm-caused depressions in tree growth from all other agents causing similar changes must be developed. Variations in the intensity of outbreaks and reports on the activities of other inimical agents in these areas may be exploited for this purpose. Stem analyses may also be combined with this data to estimate growth losses (Thomson and Van Sickle 1980; Ferrell and Scharpf 1982).

The meteorological instrumental record covers the entire region and period covered by the defoliation record. Kemp (1983) coupled these records to identify meteorological variables associated with regional outbreak frequencies.

The historical record is inadequate to evaluate long-term trends and validate models of outbreak behavior. By extending this record in certain strategic locations, it may be possible to test the effect of climatic changes and other geological processes on the initiation, maintenance, and collapse of budworm outbreaks. The large, long-lived trees and varied environments occupied by western forests (cf. Fowells 1965) must contain rich tree ring records. With crossdating, these records may be extended beyond the histories represented in living host trees. Together with the detailed climatic reconstructions developed by the Laboratory of Tree Ring Research for the West (Fritts 1976), these chronologies would provide an unparalleled opportunity to analyze the effects of climatic change on budworm population change.

Living host trees may be as old as 500 years, thus as a minimum, the record would extend to the beginning of "The Little Ice Age" and cover the period of recovery to a more benign climate (cf. Ford 1982). Should we be successful in discovering such a series, answers to such questions whether the frequency and extent of outbreaks are increasing could be provided with a measure of reliability. Contrasts with eastern chronologies developed by Blais (1983) may allow formulation of a general theory for the causes of North American spruce budworm outbreaks. By dissecting budworm defoliation time series with the use of methods described by Rust and Kirk (1978), it may be feasible to isolate effects of trends in climatic change from those of climatic cycles driven by astronomical events. The understanding derived from these studies would allow us to model budworm population behavior under future environments. These might include budworm responses to: different fire management policies, elevated temperatures due to the greenhouse effect caused by increasing atmospheric carbon dioxide concentrations, a colder climate resulting from increased atmospheric particulate densities.

Literature Cited

Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can J. For. Res. 13:539-547.

Dolph, R.E. Jr. 1980. Budworm activity in Oregon and Washington 1947-1979. U.S. Dep. Agric., For. Serv., Pacific Northwest Region, Portland, OR. Rep. 33. 54 p.

Ferrell, G.T. 1980. Growth of white firs defoliated by Modoc budworm in northeastern California. U.S. Dep. Agric., For. Serv., Pacific Southwest For. & Range Exp. Stn., Berkeley, CA. Res. Pap. PSW-153. 9 p.

Ferrell, G.T.; Scharpf, R.F. 1982. Stem volume losses in grand fir topkilled by western spruce budworm in Idaho. U.S. Dep. Agric., For. Serv. Pacific Southwest For. & Range Exp. Stn., Berkeley, CA. Res. Pap. PSW-164. 10 p.

Ford, M.J. 1982. The changing climate: responses of the natural fauna and flora. George Allen and Unwin. London. 190 p.

Fowells, 1965. Sivics of forest trees of the United States. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. No. 271.

Fritts, H.C. 1976. Tree rings and climate. Academic Press. New York. 567 p.

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of the western spruce budworm in the American northern Rocky Mountain area from 1922 through 1971. U.S. Dep. Agric., For. Serv., Intermountain For. & Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-20. 144 p.

Kemp, W.P. 1983. The influence of climate, phenology, and soils on western spruce budworm defoliation. Ph.D. Dissertation. University of Idaho. Moscow, Idaho. 143 p.

Morris, R.F. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. Can. J. Zool. 33. 225-294.

Rust, B.W.; Kirk, B.L. 1978. Inductive modeling of population time series. Pages 154-192 *in* H.H. Shugart Jr., Time series and ecological processes. SIAM-SIMS Conf. Series. Soc. Indust. and Appl. Math., Philadelphia.

Thomson, A.J.; Van Sickle, G.A. 1980. Estimation of tree growth losses caused by pest activity. Can. J. For. Res. 10: 176-182.

Williams, C.B. 1967. Spruce budworm damage symptoms related to radial growth of grand fir, Douglas-fir, and Engelmann spruce. For. Sci. 13: 275-285.

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Interpretation of the Historical Pattern of Western Spruce Budworm Outbreaks in British Columbia in Relation to Weather

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There are two distinct areas where outbreaks of western spruce budworm occur in British Columbia; one is centered around Pemberton with a high frequency of outbreaks and the other centered around Hope with a low frequency of outbreaks. The Anderson River area, which lies between these two areas, shows an intermediate frequency of outbreaks. The widespread onset of defoliation within an area in a single year suggests that initiation of an outbreak is related to weather. Similarly, the widespread disappearance of defoliation within an area in a single year, regardless of the composition and defoliation history of particular stands, suggests that outbreak collapse is related to weather.

Method of Study

The relation of long-term weather records from the Hope and Pemberton areas to appearance and disappearance of area-wide defoliation was investigated. No attempt was made to relate weather to the level of fluctuation in population density, or to percentage of defoliation. For each year of a weather record, accumulated heat units were used to define dates of budflush and stages of western spruce budworm development. These dates vary widely from year to year. Weather acting on specific stages of budworm development, as well as during specific periods of the year, was determined. Degree of synchrony of larval emergence and budflush was also determined (Thomson et al. 1984). Heat unit requirements for Douglas-fir budflush, used in the above study, were estimated from historical records (Thomson and Moncrieff 1982). The method of extrapolating from weather stations in the valley bottoms to locations at higher elevations was described by Thomson et al. (1983).

Results

Outbreaks were associated with warm dry summers in conjunction with synchrony of larval emergence and budflush. Collapse of the last two outbreaks was clearly associated with extreme high temperatures following moth flight and oviposition. Collapse of two earlier outbreaks may have been due to asynchrony between larval emergence and budflush.

Conclusions

The two areas of outbreak in British Columbia have quite different patterns of weather, one being under coastal influence and the other under the influence of interior conditions. The different probabilities of warm summers, optimal larval-host synchronization, and extreme warm temperatures following moth flight determines both the expected frequency and duration of outbreaks in the two regions.

Literature Cited

Thomson, A.J.; Moncrieff, S.M. 1982. Prediction of bud burst in Douglas-fir by degree day accumulation. Can. J. For. Res. 12:448-452.

Thomson, A.J.; Harris, J.W.E.; Silversides, R.H.; Shepherd, R.F. 1983. Effects of elevation on the rate of development of western spruce budworm (Lepidoptera: Tortricidae) in British Columbia. Can. Entomol. 115:1181-1187.

Thomson, A.J.; Shepherd, R.F.; Harris, J.W.E.; Silversides, R.H. 1984. Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia. Can. Entomol. 116:375-381.

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Historical Records Suggest a New International Strategy of Management for the Spruce Budworm in North America

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Seventy-five years of mapping spruce budworm (*Choristoneura fumiferana* (Clem.)) infestations (de Gryse 1947; Brown 1970; and Kettela 1984) and associated sampling have revealed 10 characteristics of infestation dynamics (Sippell 1984). These characteristics complement a growing body of evidence in support of the hypothesis that new infestations arise through the movement of progeny from existing active infestations (damaging populations).

Three examples of supporting evidence are: 1) infestations cover some forested areas where conditions for survival are considered so unfavorable that populations could not possibly have developed there without influx from outside; 2) new infestations appear abruptly, downwind of previously heavily infested forests; and 3) infestations in many spruce- and fir-growing areas of Canada and the United States develop exclusively during or following historic times when damage has been extensive and severe in adjacent forest lands.

This hypothesis was slow to develop and could not be reasonably advanced until the enlightening work on moth dispersal by Greenbank et al. (1980). However, it is now possible to explain the appearance of new infestations and the accompanying progressive eastward and southward spread of infestations, from Ontario and Quebec into the Maritime provinces and Newfoundland; from Minnesota into Wisconsin and Michigan; and from various sources into New York, Vermont, Maine, and other states.

Recognition of this high mobility of spruce budworm draws attention to the vital importance of active infestation in the inception of full-scale outbreaks and suggests a strategy of outbreak prevention by monitoring all lingering infestations and treating burgeoning ones while they are still relatively small.

The pre-emptive treatment of epicenters is not a new concept. What is new is the recognition, based on historical evidence, that outbreak eruption originates from within existing infestations, and that once initiated, outbreaks persist, spreading into jurisdictions where infestations would not otherwise occur.

Application of this strategy for controlling outbreaks would be international in scope, beginning in provinces and states in the western part of the range of the spruce budworm, aimed at the abatement of all infestations that threaten to rise above population levels at which moths would emigrate. Implementation would not begin until after the decline of the western segment of the present outbreak, but the time to plan is now when the need is apparent, i.e., when dead fir and spruce are present from western Ontario to Newfoundland. Such international action might be difficult to arrange but would be publicly acceptable because it would limit, and maximize, the benefits of direct control action. Also, responsibilities would be interrelated and shared. Meanwhile, specific research is needed to fill gaps in our knowledge of moth dispersal that might mitigate against the intelligent planning of coordinated action.

In this strategy lies real hope of breaking the prolonged succession of devastating outbreaks that have plagued our two countries for over two centuries.

Other forest lepidopterans show similar shifts of infestation in the direction of prevailing winds, such as the jack pine budworm (*Choristoneura pinus pinus* Free.) and the forest tent caterpillar (*Malacosoma disstria* (Hbn.)). The same behavior might be looked for in the western spruce budworm.

Literature Cited

Brown, C.E. 1970. A cartographic presentation of spruce budworm, *Choristoneura fumiferana* (Clem.) infestation in eastern Canada, 1906-1966. Can. For. Serv., Ottawa, Ont. Publ. 1263. 5 p.

de Gryse, J.J. 1947. Noxious forest insects and their control. Pages 389-400 *in* Canada Yearbook, 1947, Ottawa, Ont.

Greenbank, D.O.; Schaefer, G.W.; Rainey, R.C. 1980. Spruce budworm moth flight and dispersal, new understanding from canopy observations, radar and aircraft. Mem. Entomol. Soc. Can. 110, 49 p.

Kettela, E.G. 1984. A cartographic history of spruce budworm defoliation 1967 to 1981 in eastern North America. Can. For. Serv., Ottawa, Ont. Inf. Rep. DPC-X-14. 9 p.

Sippell, W.L. 1984. Planning now to reduce, postpone or prevent the next spruce budworm outbreak. Pages 59-67 *in* Proc. of Symposium: New and improved techniques for monitoring and evaluating spruce budworm populations. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE 88.

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Collapsing Budworm Populations

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Variation in spruce budworm population levels have been divided into recognizable phases: endemic, buildup, epidemic and decline or collapse. Of peculiar interest to people studying spruce budworm populations has been the collapse of spruce budworm outbreaks over fairly large regions, such as several provinces or states. Not until the last few years has it been generally recognized that the collapse occurs between the fourth- and sixth-instar larval stages, and if it was recognized, the proper emphasis was not given nor were its implications considered. That the collapse occurred in the mid- to late-larval instars is difficult to glean from the pre-1970 literature, including Morris (1963). However, what information can be inferred from some publications and from other authors does not contradict the conclusion that collapses have occurred during the free-feeding larval stages.

In Newfoundland the spruce budworm outbreak population collapsed in most of the Island in 1981. In 1982 the collapse continued in the peripheral areas of remnant populations, and in 1983 there was complete population collapse in some small areas though local pockets of high populations remained. Observations in each of the 3 years when some populations collapsed are recorded in this report.

In 1981 populations were high to very high throughout the outbreak area of about one million ha (2.5 million acres), and severe defoliation was expected. Overwintering larvae became active about 2 weeks after budbreak of fir; the first time that such an asynchrony occurred. The few larvae that became active at the normal time of budbreak fed and developed normally. Also, the third instar of the late-comers appeared to feed normally. However, towards the end of June these larvae appeared sluggish, little feeding was observed and normal feeding tunnels were rare. Another unusual phenomenon was that larvae would drop readily from the branches with only very slight disturbance of the branches. From June 28 to July 6 a very rapid drop in population occurred (>80 percent), when most of the population was in the fourth or fifth instar. A small proportion of the population (about 15 percent) that had reached the sixth larval instar by that time also decreased in number. Samples collected on July 6 contained very few live larvae and also very few dead larvae. Larvae in the field disappeared, which has different implications than if larvae had "only died."

Though moderate and severe defoliation still occurred in Newfoundland on 380 000 ha (1 million acres) that year, examination of branches showed that almost all feeding had been done by early instar larvae. This conclusion was based on the configuration of damaged needles, the lack of large frass pellets, and the lack of feeding tunnels.

Larvae were collected weekly from several areas for laboratory rearings. Some larvae were parasitized, some larvae died of several diseases, but on the average, 30 to 40 percent of these larvae died of unknown causes. The proportion dying of unknown causes varied with date of collection. It tended to be low during early June (10 to 20 percent), rose sharply during late June (up to 90 percent) and dropped to very low levels (0 to 10 percent) during late pupal collections. The high proportion of death by unknown causes in samples collected in late June correspond in time with the rapid drop in larval population levels observed in the field. Some of these larvae were checked for nonoccluded viruses but none were found.

Populations that collapsed in 1982 also became active 2 weeks after budbreak of fir, however, their behavior was normal, feeding was normal, larvae appeared healthy, were not easily dislodged from the branches, and generally the population reached the sixth larval instar. Deviations from normal were then observed. Each larva seemed to form several feeding tunnels without feeding. In areas of collapse 80 to 100 percent of the feeding tunnels were empty without evidence of feeding and pupae were few. Again, dead larvae or pupae were surprisingly rare, and most of these had died of unknown causes. At the time of the rapid collapse in one area, 200 larvae were collected and checked for nonoccluded viruses with negative results. Also, feeding healthy larvae on artificial diet contaminated with ground-up larvae of a collapsing population failed to produce greater mortality than larvae fed on uncontaminated diet.

Observations in 1983 were fewer than in the previous 2 years because few pockets of populations remained and only some of these collapsed. Again, overwintering larvae became active about 2 weeks after budbreak in populations that decreased rapidly later in the season. In 1983 very few fifth instar larvae occurred and populations collapsed during the third and fourth instar. As in 1981, a large proportion of laboratory-reared larvae died of unknown causes.

The cause of the collapse in all 3 years still remains a mystery. Unusual or abnormal weather patterns were not detected for any of the 3 years, and any direct or simple indirect effect of weather on budworm populations can be eliminated as the cause. Parasites were not the cause, nor any known or recognizable disease, including sporidia. No predator causing significant mortality was found, though it must be admitted that sample areas were not checked between midnight and seven in the morning. However, because laboratory-reared larvae died at the same time as field populations "disappeared," predation was unlikely as the cause of the collapse.

Royama (1984) came to the same conclusion I did and has called the unknown cause the "fifth agent" (also known as Nielson's syndrome). I cannot rule out nonoccluded viruses on the evidence available, but the cause seems to act like a vertically transmitted (= from parent to offspring) disease. Régnière's (in press) mathematical model gave evidence that such a factor could theoretically explain the collapse. However, it still remains to be demonstrated.

Literature Cited

Morris, R.F. 1963 (ed.) Dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31, 324 p.

Régnière, J. (In press.) Vertical transmission of diseases and population dynamics of insects with discrete populations: A model. J. Theor. Biol.

Royama, T. 1984. Population dynamics of the spruce budworm, *Choristoneura fumiferana* (Clem.) Ecol. Monogr. 54(4): 429-462.

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Interpreting Historical Records

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Historical records on the behavior of populations of the spruce budworm (*Choristoneura fumiferana* (Clem.)) in North America have been derived from a variety of sources. The most important of these are tree ring analyses (see Blais 1985) and defoliation/mortality or other surveys (such as obtained by the Canadian Forestry Service Insect and Disease Survey program). However, spruce budworm population changes occurring at a low or medium densities are not readily detected by these survey methods. Because of this, population changes appear to be very abrupt between undetectable levels and severe epidemic levels. By far the most extensively used technique to trace the progress of spruce budworm epidemics has been the preparation of series of maps depicting areas of severe defoliation or tree mortality. Such maps further accentuate the illusion of black-and-white, sudden changes in spruce budworm densities between endemic and epidemic levels.

Series of these maps also show a seemingly gradual expansion of outbreak areas during the development of an epidemic, much as if an epidemic front was advancing into adjacent endemic populations. During the decline of an epidemic, the maps seem to illustrate a corresponding retreat. Neighboring populations of spruce budworm are linked together by two important factors: moth dispersal, which effectively blends populations, and weather patterns, which are usually correlated between geographically adjacent areas. As a result, there is bound to be a certain degree of synchrony in changes of population density over fairly large geographical areas. Current survey methods are so poor at detecting changes at lower densities that we have a tendency to assume that spruce budworm populations are held at fairly constant low endemic levels over long periods of time until a change in conditions releases them, whereupon they expand rapidly to epidemic levels.

Spruce budworm epidemics are usually accompanied by widespread mortality of host trees. Although it is clear that spruce budworm epidemics subside even when there is still available food around, many authors maintain that lack of food is the cause of outbreak "collapses."

Looking at these historical records with no *a priori* concept of the mechanisms of population dynamics which produced them, can be very misleading. Indeed, one can imagine any number of schemes which would have as a major consequence one or more of the essential aspects of these historical records. Various authors have emphasized different aspects of the records to support their speculation. None of the interpretations of historical records presently available (e.g., Blais 1983; Hardy 1983; Sippell 1984) has been accompanied by a detailed account of the processes underlying population dynamics that is required for critical evaluation of such interpretations. However, it seems that the double-equilibrium theory of spruce budworm dynamics first introduced by Morris (1963) is a common thread in the thoughts of most authors.

There are a few sets of detailed long-term data on specific spruce budworm populations: the Black Sturgeon Lake and Chapleau areas in Ontario, the Green River data, and the egg-mass survey data of New Brunswick, as presented graphically by Royama (1984). These sets of data indicate that spruce budworm densities change in a gradual, cyclical manner (both during the rising and declining phases), along a continuum of densities. The Green River life tables, as re-analyzed by Royama (1984), indicate that this cyclicity is underlain by two distinct yet complementary mechanisms. The first is a gradual and pronounced change in larval survival, which is responsible for the long term (30-40 year) rise and fall of spruce budworm populations (the cycle). The second is moth dispersal, which is affected very strongly by weather, and acts as a strong source of stochastic influence on the progress of an otherwise regular cycle in spruce budworm density. Available knowledge suggests that population cycles over vast expanses of territory are well, although not perfectly, synchronized by moth dispersal and weather factors. More systematic factors related to site and stand conditions may contribute to slightly different timing of events in adjacent populations. Such small discrepancies in synchrony coupled with the strong bond of moth dispersal, may create the illusion of physical spread of outbreaks, particularly when low resolution techniques are used for monitoring. It is not clear, at this point, what mechanisms are involved in the cyclical behavior of larval survival, and what features of historical records can or cannot be accounted for by these mechanisms. Nevertheless, the Canadian Forestry Service scientists actively studying spruce budworm population dynamics believe that it will be more useful to seek an explanation of historical records from basic knowledge of the underlying mechanisms, rather than the other way around.

Literature Cited

Blais, J.R. 1984. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13:539-547.

Blais, J.R. 1985. The ecology of the eastern spruce budworm: A review and discussion. Pages 49-59 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworm research. Proc. CANUSA Spruce Budworms Research Symp., 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Hardy, Y. 1983. The epidemiology of the current spruce budworm outbreak in Quebec. Forest Sci. 29:715-725.

Morris, F. 1963. Conclusion. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 33.

Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. Ecol. Monogr. 54(4):429-462.

Sippell, W.L. 1984. Planning how to reduce, postpone and prevent the next spruce budworm outbreak. Pages 59-67 *in* Proc. of Symposium: New and improved techniques for monitoring and evaluating spruce budworm populations. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-88.

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Summary

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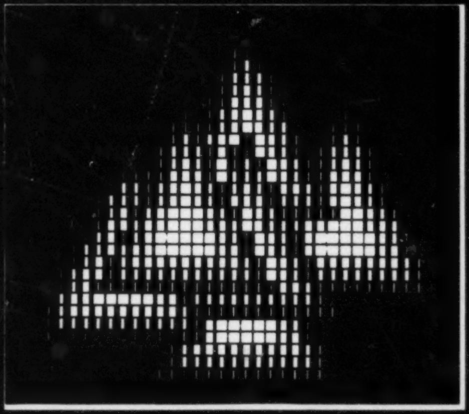
In the east several attempts have been made to correlate the occurrence of outbreaks with weather parameters. None have produced convincing correlations, and the question has been raised whether the trends in climate necessary to produce outbreaks are real, or whether they are artifacts produced by the analyses.

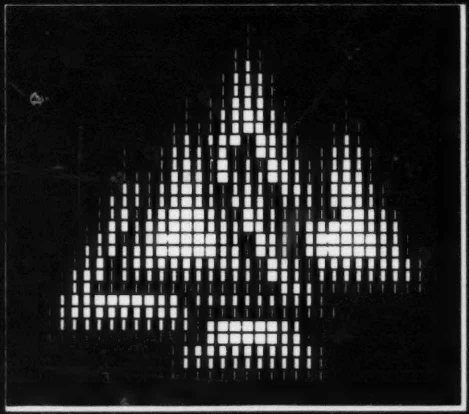
Sippell reviews the cartographic history in eastern North America and concludes that outbreaks are caused by the spread of migrating moths from existing, "relict" populations. Blais presents evidence that outbreaks in the east begin in extensive stands of mature balsam fir, but their collapse is generally associated with food depletion. However, Raske documents a specific instance in Newfoundland, where a population collapsed from "unknown causes" while food was still abundant. This and similar examples, have caused Régnière and others to look for alternative explanations of population regulation. As Régnière points out, survey methods upon which cartographic histories are based, do not detect changes in density below the level at which defoliation is visible, a problem with both eastern and western records. The available data from actual population counts indicate that populations fluctuate in the east on a 30-40-year cycle. However, as Fleming points out, these data are sparse, and the analyses based upon them assume that over time all interacting factors fluctuate together in synchrony on the same time scale, which is questionable.

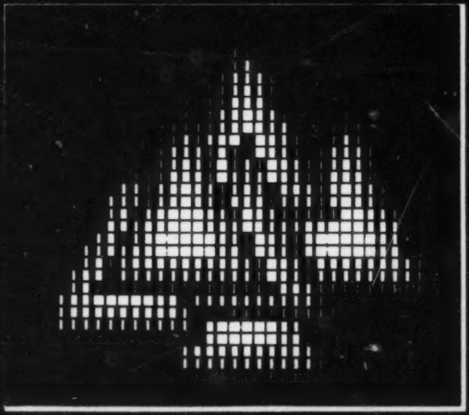
Clearly no single interpretation yet explains all the events of the past. The extensive work in correlating budworm outbreaks with climate, site, and stand characteristics has indicated some of the possible mechanisms. Only by more basic research into these mechanisms will we be able to distinguish cause from correlation leading to a complete understanding of how and why budworm populations, east and west, erupt into outbreaks.

Spruce budworm outbreaks in eastern North America have been detected by Blais from tree-ring analyses dating back to the 18th century. Records in the west do not date back so far, but, as Volney points out, the long-lived western host-tree species offer considerable scope for extending the record further back in some detail.

Western workers are agreed that weather parameters are correlated with the rise, fall, and severity of outbreaks. In British Columbia, Thomson reports that population increase is associated with warm, dry summers, but population collapse is often associated with hot weather following moth flight. In the United States interior, Kemp shows that areas which are drier with cool temperatures during moth flight have more frequent outbreaks, and also that colder winter temperatures are associated with the occurrence of outbreaks, possibly because larval survival over winter is higher under colder, nonfluctuating temperatures. Another mechanism by which weather and local climate can affect populations, which is being explored by Shepherd and Thomson, is the synchrony of budflush and larval development. Climate may also act through its effects on the vigor and nutrient status of the host trees. As Stoszek and Mika point out, tree condition is affected by site and stand characteristics acting through such factors as nutrient availability and uptake, and they suggest that budworm outbreaks in the United States interior are associated with forests under nutrient stress.







Part II

Economic and Social Impacts of Spruce Budworms in North American Forests

Effects of Spruce Budworm Outbreaks on Forest Growth and Yield

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Forest management planning and decision-making are largely based on forecasts of productivity or projections of forest growth and yield for specific areas. Most forests are managed on a sustained yield basis; annual harvest is calculated from projected timber supply. Budworm defoliation reduces forest productivity, and must be taken into account in yield projections, which requires data to quantify the relationships between defoliation, growth loss, and mortality. Program research — eastern and western — on the influence of budworm on the wood-producing capacity of forests and on forest management planning are reviewed. Because of the dearth of reliable impact data this was a primary objective of the program. Considerable progress has been made; the relationships between defoliation and growth and yield are much better quantified now than in the mid-1970s. Specific areas, however, need further work. These are described.

En aménagement forestier, la planification et la prise de décisions se fondent en grande partie sur les prévisions de la productivité ou les projections de la croissance et de la possibilité forestières de régions données. La plupart des forêts sont aménagées en fonction d'un rapport soutenu. Les dégâts de la tordeuse y réduisant la productivité, il faut en tenir compte dans les projections, ce qui exige des corrélations chiffrées entre la défoliation, le ralentissement de la croissance et la mortalité. La recherche menée dans l'Est et l'Ouest sur l'influence de la tordeuse sur l'aptitude de la forêt à produire du bois et sur la planification de son aménagement est examinée. Son objectif principal était de remédier au manque de données fiables. L'acquis a été considérable: les corrélations entre la défoliation, la croissance et la possibilité sont beaucoup mieux mesurées maintenant que dans le milieu des années 70. Toutefois, dans certaines régions, qui sont décrites, il reste du travail à faire.

Introduction

Outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) and western spruce budworm (*Choristoneura occidentalis* Freeman) occur in widespread areas of host forest across much of North America. When insects defoliate a tree, they remove a portion of the photosynthetic factory as well as sites where chemicals such as growth hormones are produced, and this affects many vital functions. Defoliation is known to result in the loss of wood production, tree mortality, and decreased stand yield (e.g., Kulman 1971). This is not new information; data on losses caused by spruce budworm were published 60 years ago by Craighead (1924, 1925) and Swaine and Craighead (1924). Why then the current emphasis on impact of spruce budworms on North American forests?

Economic impacts caused by budworm outbreaks can affect forests over millions of hectares. For example, an estimated 720 million m^3 (200 million cords) of wood was killed in eastern Canada during the 1910-1920 outbreak (Swaine and Craighead 1924). Budworm outbreaks therefore can seriously disrupt long-term timber supply, upon which the survival of forest industries is based (see Bible 1985). The spruce budworm is the most important insect or forest management problem in much of eastern North America.

In this paper, I will review the effects of defoliation by spruce and western spruce budworms on tree and stand growth and yield. My emphasis will be on influences of budworm on the wood-producing capacity of the forest and on forest management planning, as opposed to such things as physiological effects on trees, aesthetic or recreation effects, and wildlife. I will compare and contrast effects on western and eastern forests (although the paper will probably reflect my eastern perspective), and by considering research results in both the pre-CANUSA (before 1978) and CANUSA (1978-1984) time periods, will attempt to highlight what has been learned during the CANUSA Program.

Budworms, Timber Supply, and Forest Management Planning

The budworm "problem" exists only because of competition between man and the insect for the same forest resource (Baskerville 1976). Outbreaks of these insects are not a new phenomenon. Data from historical records and tree-ring analyses have clearly documented periodic, recurring budworm outbreaks, nine of which are thought to have occurred between 1710 and 1982 in eastern Canada (Blais 1958, 1965, 1968, 1983a). Outbreak recurrence has also been demonstrated in western North America based on tree ring analysis (Alfaro et al. 1982; Carlson and McCaughey 1982; Harris et al. 1985); for the whole of British Columbia, six infestations have occurred since 1909 (Harris et al. 1985).

Forests regenerate even after severe budworm outbreaks. Stands are not "destroyed" in an ecological sense, but are recycled to a younger age class. Only in this century have budworm outbreaks been more than a nuisance or curiosity, at first because of concern about damage to spruce (*Picea* sp.) sawlogs, and in the last 35-40 years because of extensive damage to balsam fir (*Abies balsamea* (L.) Mill.) and spruce pulpwood. Now, however, there is considerable concern about long-term timber supply in New Brunswick, Maine, British Columbia, and other regions, which results from both the current age structure of the forest and damage inflicted by budworm (e.g., Baskerville 1982; Reed and Associates Ltd. 1978; Sewall Co. 1983; British Columbia Ministry Forests 1980).

Forest management planning and decision-making are largely based on forecasts of productivity of the resource, or projections of forest development and timber supply in the future for specific areas (Hall 1981). Most forests are currently managed on a sustained yield basis, whereby the annual allowable (or sustainable) harvest is calculated from the projected timber supply. If budworm defoliation is reducing productivity and killing trees and stands, this must be taken into account in yield projections, which in turn requires data quantifying the relationships between defoliation, growth loss, and mortality. This has been the primary thrust of budworm impact research during the CANUSA Program, to provide data for management planning and the design of protection programs.

What Budworm Impact Data Are Needed?

In short, data on growth loss, mortality, and stand yields are needed for 1) different degrees and time sequences of defoliation, 2) different tree species, and 3) various age classes and structures of stands. Effects may also vary with site, geographic differences, and other factors. Severity of defoliation varies from removal of a little to all of the current foliage ("light" to "severe"), may include backfeeding (defoliation of older age classes of foliage) when budworm populations are very high, and takes place during several years of an outbreak. The more important host tree species include balsam fir, white spruce (*Picea glauca* (Moench) Voss), red spruce (*Picea rubens* Sarg.), and black spruce (*Picea mariana* (Mill.) B.S.P.) in the east, and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmanii* Parry), and western larch (*Larix occidentalis* Nutt.) in the west. Age classes of stands include regenerating, immature, mature, and overmature stages, and effects of budworm defoliation are known to vary among at least some of these classes (MacLean 1980). Ideally, data on growth loss and mortality resulting from each of the various combinations of defoliation, tree species, age class, etc. should be determined, but realistically, only a limited subset of these combinations will ever be studied.

A Canadian Forestry Service (CFS) Task Force into research on the spruce budworm in eastern Canada identified ten research goals, of which two dealt directly with effects of budworm on growth and yield:

> "Goal 1. To devise rules combining spruce budworm abundance and its impact on the host trees, compatible with provincial inventory/management systems, which will allow the forest manager to predict annually within his operational unit the amount and location of tree mortality up to 5 years ahead." and
>
> "Goal 4. Using provincial forest data to provide methods by which forest managers can forecast wood production, as it is influenced by the spruce budworm, for up to 10 years ahead." (Canadian Forestry Service 1979).

Several other research goals involve related subjects, including the study of deterioration of budworm-killed trees, fire behavior in budworm-damaged stands (see Stocks 1985), definition of susceptibility and vulnerability of stands to budworm, and the use of models to evaluate alternative strategies for dealing with the budworm problem. The Task Force attempted to establish a rationale that would bring research more into line with the needs of forest managers, by 1) discussing the budworm problem with forest managers in each of the six eastern provinces in Canada, 2) identifying the problem as seen from the manager's viewpoint, and 3) formulating research goals, which if met, would allow managers to better cope with the problem. In my opinion, the research goals identified by the CFS Budworm Research Task Force still represent key areas of budworm impact research. Any budworm researcher with an interest in producing results for real-world, forest management application would do well to keep the Task Force goals in mind when designing his or her research program, particularly in eastern Canada.

Effects of Budworm Defoliation on Tree Growth

Budworm defoliation affects tree growth in several ways that reduce wood production. Annual ring width is substantially reduced, to the point that radial increment data can be used to identify and "index" the severity of past budworm outbreaks (Blais 1962; Carlson and McCaughey 1982). Height growth is reduced or ceases completely through destruction of the leader (terminal shoot) of the tree (e.g., Van Sickle et al. 1983). Mortality of the uppermost whorls (top-killing) commonly occurs during outbreaks, resulting in shorter surviving trees, deformation of stems, and entry of decay organisms. Collectively, all these factors reduce volume increment of affected trees.

Methodology — The Measurement of Budworm Effects on Tree Growth and Stand Yields

Experimental design, plot layout, sampling intensity, and methods of analysis have all varied considerably among studies of budworm impact, as would be expected. Common themes run through the methodology of all studies, however, and based on several recent analyses, it is possible to make some general recommendations regarding future studies. This section is not meant to be exhaustive, but more of a brief survey of methodology.

Features which are common to most budworm impact studies include the measurement of defoliation, determination of growth rates of sample trees during the period of defoliation, and estimation of "potential" growth rates, had the defoliation not occurred.

Defoliation Measurement

Defoliation measurement in growth loss studies is usually conducted using one or more of four methods: 1) ocular defoliation estimates for individual tree crowns, sections of crowns, or individual branches, based on a light-moderate-severe scale or percentage defoliation classes (usually carried out by an observer using binoculars); 2) quantitative defoliation estimates for sampled branches from individual trees, based on rating all or a subset of the current shoots on the branch in percentage defoliation classes ("shoot-count" or Fettes method — Fettes [1950]); 3) nondestructive estimation of potential foliage biomass using relationships between number of shoots per branch, average shoot length, and average needle length (Piene 1983), combined with measurement of defoliation of individual shoots (Piene et al. 1981); and 4) destructive determination of actual foliage weight remaining after budworm feeding and comparison with estimated normal foliage weight (Kleinschmidt et al. 1980a,b). Ocular and shoot-count defoliation estimation techniques have been used in most studies. Shoot-count techniques are more accurate (and more time consuming) than ocular techniques, but a recent comparison of the two methods showed that ocular estimation is a viable technique that can give accuracy within the limits required for surveys and many research applications (MacLean and Lidstone 1982).

If possible, defoliation should be estimated on individual trees in permanent plots for each year of the budworm outbreak. Although this has not been done in many studies, it is much more satisfactory than estimating defoliation of all the age classes in just one year, because in the latter case, it is impossible to separate the effects of current defoliation, backfeeding (if population levels are high), and natural needle fall. For detailed studies of growth loss, nondestructive estimation of foliage biomass by age class (Piene et al. 1981) should be considered in addition to defoliation estimation, because foliage production relationships are altered by budworm feeding (e.g., Batzer 1973a), and tree growth is a function of foliage remaining on the tree, not that removed by budworm.

Determination of Growth During the Defoliation Period

Trees maintain a record of growth within their annual rings, so it is possible to assess defoliation on specific trees throughout an outbreak, and then determine annual growth rates at the end of the outbreak. Widths of annual rings can be determined by taking increment cores from trees, or by felling trees and cutting discs from the stem. Height increment is determined by measuring interwhorl distances. Many early studies of growth loss sampled only a single disc or increment core at breast height, but recent research has shown that greater sensitivity and more detailed results are possible from sampling discs at intervals up the stem (e.g., Piene 1980; Thomson and Van Sickle 1980).

Stem analysis techniques were developed in the late 1800s (Mlodziansky 1898) and used extensively by Duff and Nolan (1953) to characterize the growth patterns of coniferous trees. This method was first applied to the study of effects of budworm defoliation on tree growth by Mott et al. (1957). Much progress in the use of stem analysis techniques has been made since then.

Dendrochronological procedures for cross-dating, standardizing, and computing tree-ring statistics are well developed (Fritts 1976), and the use of these procedures for determining radial growth of trees defoliated by western spruce budworm was described in detail by Swetnam et al. (In press). Automated, computerized systems are available to measure annual ring widths (e.g., van der Beek and Maessen 1981; Jordan and Ballance 1983; Fayle et al. 1983) and computer programs have been developed to analyse and present, graphically, stem analysis data (Fayle 1973; Thomson and Van Sickle 1980; Timmer and Verch 1983).

Accuracy of volume and volume increment estimation in relation to number of discs sampled from the tree stem has been determined by Thomson and Van Sickle (1980) and Piene et al. (1981). Specific volume increment, which is a measure of the annual volume produced relative to the cambial surface area present each year (Duff and Nolan 1957), has been shown to be a sensitive measure for assessing growth responses (Piene 1981). A major advantage of using specific volume increment to assess response to defoliation is that trees or plots with widely differing growth rates before defoliation (e.g., small versus large trees) can be directly compared (Piene 1981).

Determination of "Potential" Growth With No Defoliation

All studies that have calculated a percentage growth loss resulting from defoliation have compared actual growth during the outbreak with a "potential" or expected growth, had there been no budworm defoliation. A variety of methods have been used to estimate potential growth. In two studies, control nondefoliated trees have been maintained by annual spraying of insecticide in the same area as the defoliated plots, which allows direct comparison (Batzer 1973b, Piene et al. 1981). Occasionally, the budworm outbreak naturally provides both lightly and severely defoliated plots in the same area, allowing comparison (e.g., Baskerville and MacLean 1979). In some cases, nonhost trees within the same stand can provide information on potential growth, although the relative density of host/nonhost trees in the stand is important; nonhost trees in a low density situation often experience release (increased growth) when surrounding host trees are defoliated (Alfaro et al. 1982). In most studies relating growth to defoliation, however, potential growth must be estimated by extrapolating preoutbreak growth rates into the outbreak period. Methods of projecting preoutbreak growth were discussed by Thomson and Van Sickle (1980). Interestingly, a similar approach has been suggested for evaluating growth response to fertilization by Salonius et al. (1982): growth of each individual tree in a pretreatment period is used as the standard with which growth following treatment is compared. In several western studies, the growth model Prognosis was used to predict potential growth without defoliation (Scott and Nichols 1983[1]; Beveridge and Cahill 1984).

Studies of Growth Loss in Eastern North America

Studies on the effects of spruce budworm defoliation on radial and volume increment were previously reviewed by MacLean (1981). These and more recent studies are summarized in Table 1, including growth loss calculated as a percentage of the potential or preoutbreak growth and a brief summary of methods and sampling intensity. A total of 13 studies is available, of which 5 have been published since 1978. Most of the data concern balsam fir, with only two studies providing data on spruce. Earlier studies determined growth in terms of radial increment, while more recent analyses have generally determined volume increment. Several of the earlier studies were mainly concerned with graphically showing that defoliation caused growth loss, and did not quantify the loss of radial increment.

For the purpose of this review, I will consider budworm "outbreaks" in a fairly general sense, as time periods (roughly 10 years) during which epidemic populations severely defoliate host trees. How much growth loss does a budworm outbreak cause? Generally, a reduction of 50 to 75 percent or more in radial or volume increment can be expected for balsam fir (Table 1). Growth loss increases as an outbreak progresses, with severe defoliation causing up to 15 to 20 percent annual reduction in the first year of feeding (Piene 1980; Pedersen 1981), 25 to 56 percent in the second year (Batzer 1973b; Baskerville and MacLean 1979; Piene 1980; Pedersen 1981), and ultimately 75 to 90 percent annual losses (Batzer 1973b; Baskerville and MacLean 1979; Pedersen 1981). In outbreaks where several years of severe defoliation are followed by moderate or light feeding, annual growth loss may continue to increase for 1-2 years after defoliation declines (Archambault 1983).

The few data available support the conventional idea that damage is less severe in spruce than in balsam fir. Reduction of radial increment of red spruce was found to range from 50 to 60 percent of the predefoliation increment for trees that survived an outbreak (Craighead 1924), whereas growth losses of white and black spruce were 36 and 18 percent, respectively (Blais 1964). Clearly more data on effects of budworm outbreaks on spruce growth are required, particularly in

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[1] Scott, D.R.M., and T. Nichols. 1983. Growth impacts on host trees due to western spruce budworm defoliation on the east slope of the Washington Cascades. Final report submitted to Canada/USA Spruce Budworms Program, Pac. Northwest For. Range Exp. Stn., Portland, OR.

Table 1

Summary of studies of loss of radial and volume increment of trees resulting from defoliation by spruce budworm populations in eastern North America

Reference	Region	Tree species	Growth loss (%)	Type of growth measurement	Methods
Craighead 1924	New Brunswick, Quebec	Balsam fir Red spruce Red spruce	60-70[1,2] 50-60[1,2] 50-90[1,3]	Radial increment	Sampled 3 discs per tree from 12-14 trees of each species. Growth loss calculated in relation to ring width of the year preceding feeding.
Belyea 1952	Ontario	Balsam fir	Not quantified[4]	Radial increment	Dendrometer measurements at breast height on 94 trees, for 6 years.
McLintock 1955	Quebec	Balsam fir	60-75	Radial increment	Increment cores at breast height for about 100 trees. Growth loss calculated by comparison with growth in the 5-year period preceding defoliation.
Mott et al. 1957	New Brunswick	Balsam fir	Not quantified[4]	Radial increment	Complete stem analysis of 2 trees and partial stem analysis of 10 trees.
Blais 1958	Ontario	Balsam fir	Not quantified[4]	Radial increment	Increment cores from 50 trees in each of 6 plots.
Blais 1964	Quebec	Balsam fir White spruce Black spruce	46 36 18	Radial increment	Discs at stump height from 50 fir, 33 white spruce, and 4 black spruce trees. Growth loss calculated by comparison with growth in the 10-year period preceding defoliation.
Batzer 1973b	Minnesota	Balsam fir	25 (2nd year) 80 (6th year)	Volume increment	Stem analysis of 3 trees from each of 8 plots. Paired plot design with one plot of each pair protected from defoliation by spraying insecticide.
Miller 1977	New Brunswick	Balsam fir	27-53	Radial increment	Discs at stump height.
Baskerville and MacLean 1979	New Brunswick	Balsam fir	25 (2nd year) 36 (6th year) 75 (10th year)	Volume increment	Complete stem analysis of a defoliated tree and an undamaged tree. Growth and mortality losses of 10 plots were quantified on a per-hectare basis.
Piene 1980	Nova Scotia	Balsam fir	20 (1st year) 50 (2nd year)	Volume increment	Complete stem analysis of 25 trees that suffered differential defoliation over 2 years. Growth loss calculated by comparison with a linear projection of previous growth.

Table 1 **(concluded)**

Reference	Region	Tree species	Growth loss (%)	Type of growth measurement	Methods
Pedersen 1981	Nova Scotia	Balsam fir	15 (1st year) 56 (2nd year) 73 (3rd year) 90 (4th year)	Volume increment	Stem analysis of one defoliated and one protected tree. Growth loss calculated by comparison with a linear projection of previous growth.
Archambault 1983	Quebec	Balsam fir	54-69[5]	Volume increment	Stem analysis of 25-27 trees from each of 3 stands. Growth loss calculated by projecting pre-outbreak growth with linear regression.
Piene 1984	Nova Scotia	Balsam fir	Not quantified[4]	Volume increment	Stem analysis of one defoliated and one protected tree (results presented graphically).

[1] Range of values represents mean growth losses after 2-5 and 6-9 years of feeding, respectively.

[2] Growth loss of trees that survived the outbreak.

[3] Growth loss of trees that died during the outbreak.

[4] Graphically-presented growth data demonstrated a growth loss caused by defoliation, but the loss was not quantified in the paper.

[5] Range of maximum annual growth loss in three stands.

view of the importance of these species in regional inventories (e.g., spruce composed 57 percent of the softwood growing stock in New Brunswick in 1978 (New Brunswick Dep. Nat. Resour. 1981), and 52 percent of the volume suitable for pulpwood in Maine in 1970 (Ferguson and Kingsley 1972)).

Reduction in radial increment resulting from defoliation has been shown to be greatest in the midcrown, and least near the base of the tree (Mott et al. 1957; Williams 1967; Piene 1980). Patterns of growth loss within the stem also vary as an outbreak progresses (Piene 1980). Therefore, the results of studies based only on radial increment in the lower bole do not necessarily reflect average tree conditions. However, because increment core measurements at breast height are cheaper than whole-tree measurements, relating whole-tree growth losses from defoliation to losses at breast height and then sampling additional stands at breast height may be an efficient sampling strategy. In fact, when Alfaro et al. (1985) calculated growth for an entire outbreak period, i.e., including the years of recovery, the periodic loss did not vary a great deal from tree top to base because faster recovery within the crown partially compensated for the greater growth decline during the defoliation period.

The time lag of 2-5 years between the initial defoliation and the first growth loss observed as reduced radial increment reported in several early studies (see MacLean 1981) actually results from measuring growth in the lower stem. More recent studies have shown that effects on tree growth are evident during the first or second year of defoliation (Table 1). This emphasizes the importance of sampling at least some discs throughout the stem of trees in studies of growth loss.

The magnitude of growth loss is a function of both the severity of budworm feeding in specific years and the temporal sequence of defoliation. Piene (1980) showed that volume growth loss increased with increasing defoliation during both the first and second year of defoliation, although there was considerable variability among individual trees. Archambault (1983) found similar results in comparing growth loss among three stands which suffered differing degrees of defoliation, in that both the maximum annual growth loss and the duration of losses increased with the number of years of severe (>75 percent) defoliation.

During periods of severe budworm defoliation, height growth generally ceases and total tree height often decreases due to top-killing. Because height growth losses are included in volume increment figures (Table 1), I have not presented height data in detail, but will give several examples. Top-killing is a common form of damage, and often more than one-half of trees surviving an outbreak will have dead tops (e.g., Swaine and Craighead 1924; McLintock 1955; Batzer and Bean 1962). During an outbreak in Minnesota, height growth of defoliated trees averaged 0.5 m (19 in) whereas healthy (sprayed) trees averaged 1.3 m (4.25 ft) over the same period, a loss of 62 percent (Batzer 1973b). Average reduction of tree height during budworm outbreaks has been reported to range from 0.5 to 4.0 m (1.5 to 13 ft) (McLintock 1955; Batzer and Bean 1962; Miller 1977; Baskerville and MacLean 1979). Baskerville and MacLean (1979) studied growth recovery of stands for 20 years following a budworm outbreak in the 1950s, and noted that the height of damaged stands remained 3 to 4 m (10 to 13 ft) below the height of undamaged stands.

Top-killing of trees causes stem deformities such as forked tops, multiple tops, crooks, and sweeps, which are common in damaged stands (Raske 1981). Studies have noted from one-quarter to all surviving trees were so affected (Schmiege 1961, Baskerville and MacLean 1979). Dead tops also act as an entrance for decay fungi, and development of heart rot is virtually assured if the top is killed back to a diameter of 1.5 cm (½ in) or more (Stillwell 1956). Volume losses or declines in sawlog quality due to deformity or decay are not well quantified, but may be considerable (Raske 1981).

Studies of Growth Loss in Western North America

Data on growth loss caused by western spruce budworm outbreaks are summarized in Table 2. Several points stand out: most studies have considered effects on radial increment; only two references predate 1978, so most of the work is quite recent; and unlike the situation in the east, the data available are about equally divided between two species, grand fir and Douglas-fir.

Studies which have compared levels of growth loss suffered by grand fir and Douglas-fir have invariably found substantially higher losses in grand fir (Williams 1967; Bousfield 1979; Bousfield and Frank 1979; Brubaker and Greene 1979; Beveridge and Cahill 1984). Growth loss has been found to vary considerably, both among studies, and between different outbreak periods in the same study (Table 2). The range of radial increment reduction is 9 to 80 percent

Table 2
Summary of studies of loss of radial and volume increment of trees resulting from defoliation by western spruce budworm populations in western North America

Reference	Region	Tree species	Growth loss (%)	Type of growth measurement	Methods
Silver 1960	British Columbia	Douglas-fir	Not quantified[1]	Radial increment	Measurement of discs at breast height from 40 trees. Average radial increment presented graphically for the outbreak period, but no growth loss values were calculated.
Williams 1967	Oregon	Grand fir Englemann spruce Douglas-fir	24-41[2] 6-25[2] Negligible loss	Radial increment	Partial stem analysis (6 discs per tree) for 10-14 trees per species in each of 4 damage classes. Growth loss calculated by comparison with growth in the 10-year period preceding defoliation.
Bousfield 1979 Bousfield and Frank 1979	Idaho, Montana	Grand fir, subalpine fir Douglas-fir	9-26 1-5	Periodic annual increment	Surveys of western spruce budworm impact.
Brubaker and Green 1979	Idaho	Douglas-fir (DF) Grand fir (GF)	GF>DF[3]	Radial increment	Comparison of effects of defoliation on growth using ring-width indices (Fritts 1976). Increment cores were sampled from 59 grand fir, 19 Douglas-fir, and 24 nonhost species.

Table 2 **(concluded)**

Reference	Region	Tree species	Growth loss (%)	Type of growth measurement	Methods
Alfaro et al. 1982, 1985	British Columbia	Douglas-fir	39,17[4] 48,15[4] 28, 8[4] 69,13[4]	Radial and volume increment	Analysed 11 discs from each of 41 trees and increment cores from 25 trees. Potential growth extrapolated from pre- and postoutbreak increment (Thomson and Van Sickle 1980). Data presented are the average reduction of radial or volume increment ((potential — actual) ÷ potential) in each of 4 outbreaks.
Ferrell and Scharpf 1982	Idaho	Grand fir	60-80[5] 20-40[5] 5-11[5] 0-20[5]	Radial increment Volume loss (% of merchantable stem volume)	Discs analysed from 3 stem levels of 20 trees from each of 2 stands. Growth loss calculated for 3 separate outbreaks by extrapolating preoutbreak increment. Stem volume losses include effects of height growth reduction, stem deformity, and decay.
Scott and Nichols 1983	Washington	Douglas-fir and grand fir	35-80[6]	Squared diameter increment	One disc at breast height sampled from each of 153 Douglas-fir and 41 grand fir trees, representing a total of 26 stands. Nondefoliated growth projected using the Prognosis model, and proportional squared diameter increment calculated for each year of the outbreak.
Beveridge and Cahill 1984	Idaho	Grand fir, subalpine fir Douglas-fir, Engelmann spruce	30-40 15	Radial increment	Increment cores sampled from 85 stands. Radial increment was projected through the defoliation period by the Prognosis model, utilizing data from pre-defoliation and defoliation growth periods to calculate growth loss.

[1] Graphically-presented growth data demonstrated a defoliation-caused growth loss, but the loss was not quantified in the paper.

[2] Range of growth losses in three damage classes reflecting increased defoliation.

[3] Radial increment was compared using ring-width indices, representing relative growth rates, but actual or percentage losses were not presented. The greatest 1-year and 5-year growth losses of grand fir were about three times and 20 times those of Douglas-fir.

[4] Reduction in radial increment (first figure) and tree volume (second figure) during four different outbreaks based on the same sample trees.

[5] Range of growth loss in two sampled stands, presented separately for two different outbreaks.

[6] Maximum average reduction in proportional squared diameter increment, representing 4 and 9 years of defoliation, respectively.

for grand fir, and 1 to 69 percent for Douglas-fir. Both Alfaro et al. (1982) and Ferrell and Scharpf (1982) have noted substantial variation in loss among different outbreaks, based on analyses of past growth of the same sample trees, that is probably a function of outbreak severity.

Alfaro et al. (1982, 1985) determined that the cumulative growth loss resulting from four western spruce budworm outbreaks in a Douglas-fir stand in British Columbia was 5.5 cm (2 in) in average tree diameter, equivalent to 12 percent reduction of tree diameter or 22 percent reduction of basal area. Volume loss per tree was calculated for each infestation as 17, 15, 8, and 13 percent respectively, and the cumulative loss for all four outbreaks was estimated at 44 percent of the volume of the average tree (Alfaro et al. 1985). Engelmann spruce was examined in two studies and the 6 to 25 percent range of growth loss found was intermediate between grand fir and Douglas-fir (Williams 1967; Beveridge and Cahill 1984).

Western studies have also shown that growth losses are a function of the degree of defoliation in individual years and duration of the outbreak. Williams (1967) selected sample trees on the basis of four damage classes which reflected cumulative defoliation, and found that losses increased with damage severity. Alfaro et al. (1982) carried out one of the most detailed analyses of growth loss in relation to annual and cumulative defoliation. They found that radial growth reduction lasted for 10 years, 5 years during the outbreak and 5 years during the recovery period. Increment reduction was related to both cumulative defoliation and annual defoliation in each outbreak year, and Alfaro et al. (1982) proposed a model which predicted proportional growth as a function of defoliation in the current year (n) and the previous two years (n-1, n-2). This type of model could prove very useful in management and protection planning because it would allow prediction of increment reduction from the current defoliation level and the last two years of defoliation history. Scott and Nichols (1983)[1] also developed models relating defoliation to height and diameter growth, and found that models using potential growth, foliage estimates, and attack duration and recovery estimates explained 80 percent of the variation in diameter growth.

Several studies have examined effects of western spruce budworm outbreaks on height growth and top-killing of host trees. Van Sickle et al. (1983) found through tree dissection studies that severely defoliated Douglas-fir in British Columbia lost an average of 7.3 internodes of growth in each outbreak, of which 4.2 were destroyed or failed to grow during the feeding period, and 3.1 were existing internodes lost to dieback. Total height was reduced by 32 percent (11.4 m, 37.5 ft) and 19 percent (5.9 m, 19.3 ft) in areas that sustained four and two outbreaks, respectively. A survey of 17 stands in British Columbia indicated that 35 percent of the standing trees showed sufficient dieback to be evident from the ground (Collis and Van Sickle 1978). Bousfield (1980) examined top-kill in mixed stands in northern Idaho, and found that 13 percent of all host trees were top-killed to more than 10 percent of their crown length. Differences in the degree of top-kill occurred among the various host species: grand fir 12 percent, subalpine fir 21 percent, spruce 9 percent, and Douglas-fir 0 percent. Bousfield and Williams (1977), Beveridge and Cahill (1984), and Ferguson and Stage (unpublished data) also noted that true firs suffered the most severe damage in mixed stands whereas Douglas-fir and spruce were less damaged. Grand fir volume losses due to height growth reduction, stem deformity, and decay were found to average 11 and 20 percent in two stands in Idaho, with decay accounting for over 90 percent of the volume loss (Ferrell and Scharpf 1982). More than 75 percent of the trees were top-killed at least once in a stand that had suffered three western spruce budworm outbreaks during the last six decades (Ferrell and Scharpf 1982). Outbreaks also reduced height growth of western larch by at least 25 percent because larval feeding severed the stems of the current-year terminal and lateral shoots (Schmidt and Fellin 1973).

Effects of western spruce budworm feeding on height growth, and particularly the predisposition of damaged trees to stem deformities and decay, are probably among the most serious results of outbreaks in the west. Although total tree height can be reduced by budworm damage, merchantable height will be even more severely affected if a large defect develops during the period of tree recovery after dieback (Van Sickle et al. 1983). Defect formation may prevent the tree from producing any merchantable wood about the point of recovery, and thus could be particularly serious in young stands that conceivably could have their potential merchantable height curtailed (Van Sickle et al. 1983).

Effects of Budworm Outbreaks on Stand Volume, Increment, and Yield

Effective management of a forest resource during a budworm outbreak requires information about the effects on wood production at the stand level. To understand how defoliation affects volume production on a per hectare basis, it is first necessary to determine how individual trees react to defoliation, and then results can be extrapolated to volume loss per hectare. Methods of forecasting growth and yield of budworm infested forests are reviewed for western and eastern North America by Crookston (1985) and Seymour (1985), respectively. Studies that provide data on effects of budworm outbreaks on stand volume increment or yield are summarized in Table 3. Note that seven of the eight references are recent (post 1978), and only two references pertain to western North America.

The studies in Table 3 fall into two separate groups: four studies report effects of budworm outbreaks on stand volume increment or survivor growth, and four determine effects on stand yield. The latter studies combine effects on growth and mortality into a single yield reduction; data on tree mortality during budworm outbreaks are reviewed in the next section of this paper.

Information on stand volume increment reduction during budworm outbreaks is available from three studies in Maine and one in Quebec. Kleinschmidt et al. (1980b) studied 20 plots in Maine which represented different defoliation scenarios. A 5-year defoliation history was estimated for each plot by comparing weights of foliage in each age-class of needles with the amounts produced by nondefoliated trees; tree growth was assessed by stem analysis. Plots were grouped into several defoliation scenario classes, and results showed that stands which suffered light defoliation (<20 percent of current foliage) for 5 years showed negligible growth loss, whereas severe defoliation (90 to 100 percent of current foliage) for 5 years resulted in a 60 percent annual growth loss, or a cumulative loss of 34 percent over the 5-year period. This cumulative growth loss was equivalent to 15 m^3/ha (215 ft^3/acre) of wood production lost to the stand during 5 years of nonfatal defoliation. Kleinschmidt et al. (1980b) also showed that plots with a history of defoliation increasing from 20 to 90 percent of current foliage over 4 or 5 years suffered about a 40 percent annual growth loss, and that preventing defoliation by spraying with insecticide after several years of defoliation apparently reduced the growth loss, but only slightly. Solomon (1984) used similar methods to study effects of defoliation on volume increment in an additional 20 plots in Maine, and found that light, increasing (from 13 to 65 percent), and severe defoliation scenarios resulted in maximum volume increment reductions of 12, 36, and 47 percent, respectively.

A third Maine study is the Maine Spruce Budworm Impact Study, a cooperative effort among the CANUSA Program, U.S. Forest Service, Maine Department of Conservation, and 11 private forestry companies in Maine (Brann et al. 1983). Designed to document the impact of the spruce budworm on growth and mortality, and begun in 1975, the study involves annual measurements of over 400 plots. Data from the latest annual report of the study indicated that softwood basal area accretion (survivor growth) had decreased from 0.68 m^2/ha (3 ft^2/acre) in 1975-76 to 0.45 m^2/ha (2 ft^2/acre) in 1980-81, a loss of 35 percent due to budworm defoliation (Brann et al. 1983).

Archambault (1983) reported the reduction in cumulative (5-year) volume increment of surviving trees for three spruce–fir stands in Quebec that suffered different degrees of defoliation. Annual defoliation was determined for each year from 1974-1981 in terms of light (0 to 25 percent), moderate (26 to 75 percent), and severe (76 to 100 percent) classes; the three stands sustained severe defoliation for 2, 3, and 4 years, respectively and light defoliation thereafter. Cumulative growth losses in the three stands from 1977 to 1981 were 36, 47, and 54 percent of the potential growth, or 17-18 m^3/ha (243-257 ft^3/acre) (Archambault 1983).

Table 3

Summary of data on cumulative reduction in stand yields and loss of volume increment caused by spruce budworm outbreaks

Reference	Region	Stand type	Reduction caused by budworm %	m^3/ha	ft^3/acre	Type of growth measurement	Methods
Batzer 1973b	Minnesota	Fir-spruce	67	71	1015	Stand yield	Yield reduction resulting from both growth loss and mortality compared in four pairs of sprayed and unsprayed plots in "pole-sized" timber. Measurements carried out for 5 years during and 5 years after a budworm outbreak; 60% of the losses occurred after the outbreak.

Table 3 **(continued)**

Reference	Region	Stand type	Reduction caused by budworm %	m³/ha	ft³/acre	Type of growth measurement	Methods
Baskerville and MacLean 1979	New Brunswick	Fir-spruce	39-81[1]	120-220[1]	1714-3142	Stand yield	Ten plots measured annually during a budworm outbreak in the 1950s, and at 5-year intervals for 20 years thereafter. Stand yield reductions (including both growth loss and mortality) presented are for 10 years after the start of the outbreak, and are based on projections of stand development without budworm.
Kleinschmidt et al. 1980b	Maine	Fir-spruce	19-34[2]	7-15[2]	100-214[2]	Stand volume increment	Reduction in cumulative (5-year) volume increment determined for 20 plots suffering non-fatal levels of defoliation over a 5-year period. Defoliation history determined by comparing weight of foliage by age-class with amounts produced by nondefoliated trees; growth loss calculated by projecting preoutbreak growth with non-linear regression.
Thomson et al. 1982	British Columbia	Douglas-fir	10-36	—	—	Stand yield	Demonstration of a system for calculating and presenting actual stand volume following outbreaks as a percentage of potential stand volume. Largely based on methods of Thomson and Van Sickle (1980); values presented are for a hypothetical stand. Magnitude of yield reduction is a function of duration of outbreak and age of tree.

Table 3 **(concluded)**

Reference	Region	Stand type	Reduction caused by budworm			Type of growth measurement	Methods
			%	m³/ha	ft³/acre		
Alfaro et al. 1985	British Columbia	Douglas-fir	18	60	857	Stand yield	Losses were calculated for one stand. Mortality amounted to 39% of the stems/ha (40 m³/ha, 572 ft³/acre), and survivors lost an estimated 20 m³/ha (286 ft³/acre) during the outbreak.
Archambault 1983	Quebec	Fir-spruce	36-54[3]	17-18[3]	243-257[3]	Stand volume increment	Reduction in cumulative (5-year) volume increment of surviving trees determined for three stands. Growth loss determined by projecting preoutbreak growth of individual trees with linear regression, calculating mean growth loss by dbh class, and applying these values to the stand table.
Brann et al. 1983	Maine	Softwood (fir and spruce)	35	—	—	Accretion	Annual measurement of 412 plots in the Maine Spruce Budworm Impact Study. The figure presented is the reduction in average annual accretion (survivor growth) between 1975-76 and 1980-81.
Solomon 1984	Maine	Fir-spruce	36-47[4]	26-27[4]	372-386[4]	Stand volume increment	Study of 20 plots, using same methodology as Kleinschmidt et al. (1980b).

[1] Range of stand yield reductions based on 10 plots.

[2] Range of volume increment reduction resulting from increasing (from about 20 to 90%) and severe defoliation, respectively. Comparable annual growth losses resulting from these levels of defoliation were 40 to 60%.

[3] Range of volume increment reduction among three stands.

[4] Range of volume increment reduction resulting from increasing (from 13 to 65%) and severe defoliation, respectively.

Batzer (1973b) and Baskerville and MacLean (1979) presented data on yield reduction resulting from both growth loss and mortality, for stands in Minnesota and New Brunswick, respectively. Batzer compared four pairs of sprayed and unsprayed plots for 5 years during and 5 years after a budworm outbreak, and found a cumulative loss of 71 m³/ha (1,015 ft³/acre). This was equivalent to a yield reduction of 67 percent in these immature, "pole-sized" stands. Net mortality (level in unsprayed plots minus that in sprayed plots) amounted to 56 percent of the balsam fir and 33 percent of the white and black spruce. A significant result from the study was that 60% of the losses occurred after defoliation ceased (Batzer 1973b).

Ten fir plots studied by Baskerville and MacLean (1979) were severely defoliated in the mid-1950s, and suffered mortality of 18 to 80 percent of the total volume per hectare. Recovery of these stands was studied for 20 years following the collapse of the budworm outbreak. Stand yield reductions 10 years after the start of the outbreak were estimated to range from 120 to 220 m^3/ha (1,714 to 3,142 ft^3/acre) on the 10 plots examined, or 39 to 81 percent; calculation of these reductions were based on projections of stand development and yield without budworm damage (see Baskerville and MacLean 1979). Within 5 years of the cessation of defoliation, the crowns of surviving trees appeared fully recovered, and diameter and height growth were similar to that in unaffected stands. In subsequent years, diameter growth showed a classic response to the reduction in stand density (thinning) resulting from the budworm-caused mortality, and increased substantially beyond predefoliation levels; this was also noted by Williams (1967). However, the recovery in volume per hectare was poor because the increased diameter growth was on smaller trees (as a result of growth reductions during the outbreak) and there were fewer trees per hectare. The decreased height growth was particularly important because the defoliated trees were 3 to 4 m (10 to 13 ft) shorter than similar nondefoliated trees after the outbreak collapsed. In some situations, this could result in defoliated trees being at a competitive disadvantage to nonhost trees. Only one of the 10 plots had regained its predefoliation volume 15 years after defoliation ceased (Baskerville and MacLean 1979). Projection of stand development to age 75 years further suggested that on average, the plots which suffered mortality and growth loss caused by budworm would have only slightly more than one-half the projected volume without defoliation.

Thomson et al. (1982), considering effects of western spruce budworm outbreaks on stand yield, demonstrated a system for calculating and presenting actual stand volume following outbreaks as a percentage of potential stand volume. The magnitude of yield reduction was presented in nomogram form as a function of duration of the outbreak and tree age, which is a very effective method of presenting yield reduction results for forest managers. The values presented by Thomson et al. (1982) indicated stand yield reductions for Douglas-fir in British Columbia could range from 10 to 36 percent, but were only for a hypothetical stand. Actual losses in one stand suffering severe defoliation were calculated by Alfaro et al. (1985) to be 18 percent of the total volume per hectare (60 m^3/ha, 857 ft^3/acre). This yield reduction included the death of 39 percent of the trees (40 m^3/ha, 572 ft^3/acre) and an estimated 20 m^3/ha (286 ft^3/acre) reduction of growth in surviving trees.

Effects of Budworm Defoliation on Tree Mortality

Defoliation initially causes growth loss of trees, but persistent severe defoliation for several years will result in tree mortality. The amount of mortality resulting from budworm outbreaks is a function of several factors, including the severity and duration of defoliation, the species and age of trees involved, age-class distribution, species composition, spacing, site, and other characteristics of the stand. Studies of the vulnerability of stands to mortality during budworm outbreaks were reviewed and discussed by MacLean (1980). I will use that reference as the basis for summarizing information from earlier studies, and then will discuss results of recent research.

Tree Mortality Caused by Budworm in Eastern North America

Several studies of the amount of tree mortality resulting from budworm outbreaks have been carried out in various regions of eastern North America since the 1910s and early 1920s. The timing of mortality has generally been consistent among different outbreaks and locations, with trees usually starting to die after 4 or 5 years of severe defoliation (MacLean 1980). In less vulnerable, immature stands it may take 7 or 8 years of defoliation for the first mortality to occur. Mortality caused by budworm has usually ended by about 12 years after the start of an outbreak, with 70 to 100 percent of the trees dead in mature balsam fir stands and 30 to 70 percent dead in immature fir stands (MacLean 1980). Species and age of trees and regional differences influence mortality; in summarizing data for 100 plots from various locations, MacLean (1980) found average mortality levels of 85 percent in mature fir stands, 42 percent in immature fir stands, 36 percent in mature spruce stands, and 13 percent in immature spruce stands. The few data available indicate that black spruce is less vulnerable than red or white spruce, which in turn are less vulnerable than balsam fir (MacLean 1980).

The current spruce budworm outbreak in eastern North America started in the late 1960s in northeastern Ontario, western Quebec, central New Brunswick, and Maine. By 1975, the outbreak covered about 57 million hectares (140.8 million acres) of forest land in eastern Canada and the United States, and by 1981, about 23 million hectares (56.8 million acres) contained significant volumes of dead and dying timber (Kettela 1983). A large number of surveys and research studies have examined tree mortality caused by budworm in different regions during this outbreak. Some studies are still ongoing and only partial results are available at present; I will summarize the currently available data by region, starting with Michigan and Ontario and working east.

Michigan
A large CANUSA-funded study of spruce budworm impact in the Lake States was begun in 1978 by Witter and coworkers. Methods and field sampling techniques in the study were described by Mog and Witter (1979). A total of 199 stands has been sampled for tree mortality, stand characteristics, and site (Mog et al. 1982; Lynch, Fowler, and Witter 1984). Tree mortality varied considerably among the regions studied. In 1980, balsam fir mortality reached 93 and 54 percent in districts of the Hiawatha National Forest (eastern Upper Peninsula of Michigan), was 22 to 26 percent in the western and northern Ottawa National Forest, but was <10 percent in the central portion of the Peninsula (Mog et al. 1982). The Michigan Impact Study has also involved substantial technology transfer efforts (see Witter et al. 1982), the development of models to predict impact (Lynch, Fowler, and Witter 1984) and rate budworm hazard (Lynch, Witter, and Olson 1984), and analyses of mortality in relation to stand, site, and soil parameters (Lynch and Witter, 1985). One interesting finding of the Michigan studies was the high degree of variability among the regions studied, both in terms of the factors significantly associated with impact, and in how strong the correlations were (Lynch, Witter, and Olson 1984). The amount of preoutbreak balsam fir basal area, total basal area, and percent basal area in fir were consistently correlated with impact, while nonhost or hardwood basal area were sometimes negatively correlated with impact.

Ontario
The spruce budworm problem in Ontario was recently reviewed in a comprehensive symposium (Sanders and Carrow 1983). Both the impact of budworm on the forest, and the economic importance of that impact vary considerably among regions in Ontario. Forests in northern Ontario are dominated by black spruce, jack pine (*Pinus banksiana* Lamb.), and poplars (*Populus* sp.), while balsam fir and white spruce make up less than 10 percent of the volume (Howse et al. 1982). Fir and white spruce are utilized to a certain extent in some regions, but hardly at all in other areas (see Sanders and Carrow 1983). Thus, there is less concern about budworm impact in Ontario than in other regions where budworm host species make up the largest portion of the softwood timber supply, and only limited data are available. The overall loss of volume to budworm in Ontario has been considerable, and was estimated at about 16 million m^3 (565 million ft^3) in 1981, with mortality in sample areas of the northeast region averaging 10 to 15 percent of the white spruce, 17 percent of the black spruce, and up to 85 percent of the balsam fir (Meating et al. 1982).

Quebec
Blais (1981) studied mortality of fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Plots were remeasured annually for 5 years after the cessation of defoliation, over which time fir mortality increased from 44 to 91 percent, and spruce mortality increased from 17 to 52 percent. Thus, more than 50 percent of the trees of both species that died did so during a 4-year period after defoliation ceased. Mortality in young fir stands (20-50 years old) in this region was almost as high as in mature stands (Blais 1981). In another study, Beaulieu and Hardy (1982) determined that 55 percent of the fir trees in the Gatineau region of Quebec had been killed by budworm. Beaulieu and Hardy (1982) also presented a method of analysis which differentiates between spruce budworm caused mortality and natural mortality.

Maine
Several studies and survey assessments of mortality caused by budworm have been carried out or are ongoing in Maine, involving State, industry, and U.S. Forest Service efforts (Devine and Trial 1980). For example, Corcoran (1980) reported that on lands of Great Northern Paper Co., annual fir mortality had increased 61 percent (based on an average for the previous 5 years), annual growth had decreased 21 percent, and mortality from budworm damage was estimated at 1 million cords (2.55 million m^3). Seymour (1980) analysed mortality during an uncontrolled outbreak, and found red spruce was less vulnerable than fir: regardless of stand composition, <10 percent of the spruce died from 1977-79, compared with over 50 percent of the fir.

The Maine Spruce Budworm Impact Study (described previously) has also provided substantial data on tree mortality. In 1981, mortality had increased over 1976 levels by 173 percent and 33 percent for fir and spruce, respectively, in the softwood type (Brann et al. 1983). Mortality was found to be highly correlated with mean stand diameter, with higher mortality in stands with smaller mean diameter; this was attributed to the fact that stands with smaller mean stand diameters had a larger component of fir (Brann et al. 1983).

In an interesting study of periodic mortality rates, Seegrist and Arner (1982) used data from the Maine Spruce Budworm Impact Study and the U.S. Forest Service Maine Forest Survey to compare mortality in 1976-78 with predictions of what mortality would have been had natural mortality rates remained at levels experienced before the outbreak. They found that the annual net probability of natural mortality (before the outbreak) ranged from 0.5 to 0.9 percent per year for red and white spruce and from 1.0 to 3.8 percent per year for balsam fir, where the range reflects different mortality rates for different diameter classes. During the outbreak, mortality increased over these rates by a factor of 2.5 for both spruce and fir, and 60 percent of the cumulative mortality was attributed to the spruce budworm outbreak (Seegrist and Arner 1982).

New Brunswick

In 1980, 1220 permanent sample plots in New Brunswick were assessed by the New Brunswick Department of Natural Resources to determine damage caused by the spruce budworm to balsam fir and spruce (Clowater and Andrews 1981). Results indicated that damage to fir was much greater than to spruce and that the spruce budworm protection program had been effective in preventing mortality of balsam fir in the protected zone because damage was about one-half the level found in the unsprayed zone. Although damage to spruce was relatively light in comparison with damage to fir, spruce mortality levels were about the same in both protected and unsprayed zones (Clowater and Andrews 1981). The permanent sample plots examined in this study were also remeasured in 1983, but data are not yet available (W.G. Clowater; N.B. Dept. Nat. Resour., Fredericton, N.B., personal communication).

Tree mortality caused by budworm defoliation and the relation of mortality to tree, stand, and site characteristics, budworm hazard, and protection were also examined in a recent study of impact in spruce stands in New Brunswick (MacLean et al. 1984). Tree mortality and defoliation were measured in 45 spruce stands protected against budworm damage and in 27 unprotected spruce stands, representing a total of about 17,000 trees. Cumulative spruce mortality was relatively low in both protected and unprotected stands, averaging about 13 and 20 percent of the total volume (MacLean et al. 1984). Fir mortality was higher in unprotected than in protected stands, although fir formed only a minor component of most of the sampled stands, which were selected for their spruce content. Both average mortality and range were similar among the four spruce types present in New Brunswick: black spruce, red spruce, hybrid red-black spruce, and white spruce. In examining the relationship of tree mortality to stand and site characteristics, MacLean et al. (1984) found the strongest correlations between dead spruce-fir volume (cubic metres per hectare) and total stand volume ($r = 0.85$), and between dead fir volume and total fir volume ($r = 0.75$). No apparent relationships were observed between mortality levels and various indices of protection and budworm hazard.

Nova Scotia

A severe spruce budworm outbreak has been going on in several areas of Nova Scotia since the early to mid-1970s. Several research studies of tree mortality caused by budworm and stand vulnerability have been carried out or are ongoing, particularly on Cape Breton Island (MacLean 1979; Ostaff 1980, 1982; Pendrel 1981, 1982). As of 1982, 10 years after the start of the outbreak, the proportion of dead merchantable balsam fir was 67 percent on the Highlands, and 88 percent on the Lowlands of Cape Breton Island (Ostaff 1982). Studies of permanent sample plots in Cape Breton established in the early 1960s by the Nova Scotia Department of Lands and Forests indicated that the rate of softwood mortality more than doubled since the budworm attack, whereas the growth of the remaining living trees was reduced by about 60 percent (Bailey 1982). The cumulative effect of the mortality and reduced growth resulted in an overall loss of about 17 million m^3 (600 million ft^3) between 1975-81, with an additional 4.5 million m^3 (159 million ft^3) projected to die (Bailey 1982). Wellings and Bailey (1982) also used forest inventory data from Cumberland County, Nova Scotia, to estimate mortality losses due to budworm. Comparisons of periodic annual mortality before and during the outbreak period indicated that mortality of red/black spruce increased 102 percent and mortality of balsam fir increased 198 percent.

In addition to killing trees, budworm defoliation often makes trees more susceptible to other insects and diseases such as bark beetles and root rots. Ostaff (1983) found that the shoe-string root rot (*Armillaria mellea* (Vahl ex Fr.) Kummer) occurred in about 20 percent of balsam fir trees in Cape Breton that were defoliated 50 to 75 percent (cumulative defoliation), about 50 percent of trees defoliated 75 to 90 percent, and about 90 percent of trees defoliated 90 to 100 percent. The fungus causes root and butt decay, reduction in growth, decline in vigor, dieback of the crown, and eventually tree mortality (Ostaff 1983). Ostaff and Newell (1981) also reported that spruce beetle (*Dendroctonus rufipennis* Kby.) infestations have resulted in widespread mortality in the spruce forests of Nova Scotia, killing an estimated 18 percent of the merchantable white spruce volume, and infesting an additional 9 percent of the white spruce and 5 percent of the red spruce volume.

Newfoundland

No widespread or severe budworm outbreaks are known to have occurred in Newfoundland before the current one that began in 1971 (Otvos and Moody 1978; Blais et al. 1981; Blais 1983a). Forests in Newfoundland have suffered heavy mortality during the most recent outbreak, however, and studies are underway to document effects (e.g., Hudak and Raske 1981; Raske and Rowe 1982). In 1981, it was estimated that the total volume lost in softwood stands containing tree mortality >10 percent was 31.7 million m^3, (1.1 billion ft^3), which amounts to 18 percent of the spruce–fir inventory in Newfoundland (Raske et al. 1982). Most of these stands were in need of salvage, and contained 16.0 million m^3 (565 million ft^3) of dead trees and 2.8 million m^3 (99 million ft^3) of dying trees. Only about 30 percent of the dead and damaged volume will be salvaged, resulting in estimated losses of 22.4 million m^3 (791 million ft^3) (Raske and Sutton 1982). An analysis of tree mortality in Newfoundland in relation to tree and stand characteristics was carried out by Raske (1984).

Tree Mortality Caused by Budworm in Western North America

Western spruce budworm outbreaks and their effects were reviewed by Johnson and Denton (1975) and Carlson et al. (1983). Outbreaks have persisted for over 30 years in the northern Rocky Mountain area of the United States. About 1 to 2 million hectares (2.5 to 5 million acres) of forest, primarily in Idaho and Montana, have been infested for many of these years, although the size of the outbreak has fluctuated considerably between years and among areas (Carlson et al. 1983). The western spruce budworm has also repeatedly defoliated Douglas-fir in British Columbia, with the last infestation reaching a maximum of 226 000 ha (558,000 acres) of defoliation in 1976 (Harris et al. 1985).

Relatively few data are available to quantify the tree mortality resulting from western spruce budworm outbreaks, as opposed to data on defoliation, tree damage, etc. Johnson and Denton (1975) reviewed a large number of published and unpublished reports of outbreaks, and concluded that although host forests occasionally survived outbreaks intact or suffered substantial mortality, the damage reported in most infested forests was between these extremes. This is in contrast to effects of spruce budworm outbreaks in eastern Canada and the United States, where heavy mortality is the norm rather than the exception (e.g., MacLean 1980).

In mature, multilayered stands in the western United States, tree mortality resulting from budworm defoliation is most pronounced in the smaller, intermediate trees (Carlson et al. 1983). In a survey of 66 stands within infested forests in the Intermountain Region, Patee (1966) found that all trees killed by budworm were <23 cm (9 in) dbh, and mortality averaged 47 trees per hectare (19 per acre). Mortality in small trees is variable, however, ranging from 11 to 84 percent of the trees <13 cm (5 in) dbh in one study (Bennett 1978), but negligible in other areas (Bousfield and Williams 1977; Beveridge and Cahill 1984).

Mortality resulting from western spruce budworm outbreaks has also been examined in Douglas-fir stands in British Columbia. Collis and Van Sickle (1978) noted that tree mortality was rare in young and semimature stands, <1 percent in 16 of 20 stands examined; occasional 40- to 250-ha (100- to 618-acre) patches of higher mortality were associated with Douglas-fir bark beetle (*Dendroctonus pseudotsugae* Hopkins) attack. Johnson and Denton (1975) also reported that heavy defoliation of sawlog-size Douglas-fir trees by budworm may render them susceptible to lethal attacks by Douglas-fir bark beetle. Alfaro et al. (1982) found tree mortality resulting from a western spruce budworm outbreak was 39 percent of the number of trees per hectare, or 12 percent of the basal area, which was considerably higher than the level reported for other studies in British Columbia (e.g. Shepherd et al. 1977; Ross et al. 1978). Alfaro et al. (1982) estimated that the natural mortality rate in their stand was 0.5 percent per year. Mortality began in the 4th year of defoliation and peaked in the 7th year of the outbreak (2 years after the cessation of feeding). It was estimated that bark beetles were the primary mortality agent in only 2 percent of the trees (Alfaro et al. 1982). Differences in mortality level occurred among crown classes, with smaller, suppressed trees sustaining higher mortality; this resulted in a shift in the stand structure to a higher proportion of dominant and intermediate trees. However, tree mortality was not evenly distributed throughout the stand, but was spatially highly variable, creating an unsatisfactory thinning effect (Alfaro et al., 1984). Alfaro et al. (1982) reported that mortality of individual trees was related to cumulative defoliation level (sum of annual defoliation during the outbreak): mortality occurred only if cumulative defoliation exceeded 175 percent, and reached 80 percent in trees with more than 350 percent cumulative defoliation.

Prediction of Tree Mortality Caused by Budworm Outbreaks

Blais (1983b) discussed the prediction of tree mortality induced by spruce budworm, and concluded that reliable predictions of damage on a stand basis may not be possible because of 1) variability in the course of budworm outbreaks resulting from unpredictable and unexpected increases or decreases in population levels, and 2) variability in tree mortality resulting from defoliation, among outbreaks, geographic regions, tree species, and maturities of stands. Rather than attempting to predict mortality on a stand basis, Blais (1983b) advocated the use of general rules that pertain to budworm impact on the forest (e.g., Canadian Forestry Service 1982), and the classification of forests with respect to their vulnerability to budworm on a regional basis (e.g., Blais and Archambault 1982; MacLean 1982). Seventeen hazard and vulnerability rating systems available for predicting the risk of budworm damage in eastern Canada and the United States were reviewed and discussed by MacLean (1985). Long-term management programs in relation to budworm attack should be based on two main considerations: regional variations in vulnerability, and socio-economic consequences resulting from reductions in wood supply caused by budworm (Blais 1983b). In this way, regions with high vulnerability and a tight balance between timber supply and demand could receive priority in protection and management programs aimed at reducing losses from future budworm outbreaks.

Regarding general rules that pertain to budworm impact on the forest, it would appear from several recent analyses (MacLean 1980; Batzer and Hastings 1981; MacLean et al. 1984) that the best current model of tree mortality caused by budworm is that of a constant proportion of the total volume (i.e., a linear relationship), assuming a general "outbreak" defoliation pattern, and specifying the stand age/species characteristics. This follows for both balsam fir and spruce, but the proportion of a stand that can be expected to die during an outbreak varies considerably between these two species types. Whereas mortality of fir in mature stands is generally high (often approaching 100 percent), smaller proportions (typically one-quarter to one-half) of spruce stands and immature fir stands are killed. The presence of nonhost species has been found to reduce the level of fir mortality in some studies (Batzer and Hastings 1981; Lynch, Witter, and Olson 1984), but not in others.

An alternative method of predicting tree mortality in stands involves the use of a timber inventory method designed to identify potential tree mortality or volume losses. Such a system is currently being used by Fraser Inc. in New Brunswick as a tool in harvest scheduling (Gasson and Noble 1983). The method uses the presence and extent of a relatively few symptoms in the fir and spruce component of a stand during cruising to predict short-term volume losses. Symptoms identified on individual trees include overmaturity, cumulative budworm damage (bare top, defoliation >50 percent, backfeeding), top breakage, stem wounds, and lean (Gasson and Noble 1983). Incorporating this kind of "symptom identification" in stand cruising could have considerable potential in improving timber harvest scheduling, which is extremely important in areas with tight timber supply.

Sampling in Mortality Studies

Accuracy and precision of insect density and impact estimates were discussed by Fowler and Witter (1982). Plot size and sampling intensity in most studies of tree mortality caused by budworm have been arbitrarily chosen with little consideration of relationships between sample size and required precision. However, two recent studies have considered this question: Karpinski and Witter (1982) in Michigan, and MacLean and Ostaff (1983) in Nova Scotia. Both studies found little difference in the precision of mortality estimates from plots ranging from 0.01 to 0.40 ha, or in the case of MacLean and Ostaff (1983), prism point samples with metric basal area factor (BAF) = 2.3. In determining the number of plots per stand, Karpinski and Witter (1982) compared the precision of 2-5 plots per stand in terms of reduction of the coefficient of variation of the mean with increasing number of plots, and concluded that the largest reduction occurred when increasing from 2 to 3 plots per stand. In contrast, MacLean and Ostaff (1983) developed curves relating required number of plots to desired precision (specified as a bound on the mortality estimate), which indicated that sampling about 15 prism points within each stand should result in estimation of cumulative mortality to about ± 10 percent precision. A subsequent sample size analysis based on data from 15 prism point samples in each of 72 spruce stands in New Brunswick indicated that estimation of cumulative tree mortality to precision levels of ± 10 and 5 percent mortality would require 6 and 25 prism points (metric BAF = 2.3) per stand, on average (MacLean 1984a).

Effects of Budworm Defoliation on Seed Production and Regeneration

Budworm defoliation drastically reduces cone and seed production in severely defoliated stands, and therefore alters regeneration establishment patterns. Readers are referred to Carlson et al. (1983), Ghent et al. (1957), and Schooley (1978, 1980) for more detailed discussions of this subject in western and eastern North America. Budworm can also feed on advance regeneration present under stands suffering an outbreak. These effects can potentially alter long-term successional trends, lengthen stand rotation, change stand species composition, and reduce harvestable yields.

Spruce budworm feeding that severely defoliates trees or destroys vegetative buds results in the shortening or elimination of shoots upon which the cones develop. Production of cone buds is thus substantially reduced by 50 and 75 percent after one and two years of severe feeding for balsam fir (Schooley 1978). In fact, cone production may become impossible when defoliation for several successive years kills the principal cone-producing area of the crown. Top-killing can prevent the production of cones for several years in true fir stands (Shearer 1980). Larvae also feed directly on cone flowers and conelets after emerging from their overwintering sites (Powell 1973), resulting in less than 5 percent of cones reaching maturity on severely defoliated balsam fir (Schooley 1978). On black spruce, virtually all flowers are destroyed even when only a small population of budworm larvae are present because black spruce needles and vegetative buds are less favorable feeding sites than flowers (Schooley 1980). Other insects such as coneworms (*Dioryctria* sp.)

also damage spruce cones, compounding the effect.

Effects of defoliation on cone and seed production are dependent upon the budworm population level and severity of feeding, combined with the potential cone crop present in specific years (Powell 1973). Fellin et al. (1983) reported that 100 percent of Douglas-fir cones can be destroyed when western spruce budworm larvae are abundant, whereas Dewey (1970) determined that an average of 36 percent (range of 9 to 71 percent) of Douglas-fir cones in sampled stands were infested. Western spruce budworm was found to be the principal insect species damaging cones of Douglas-fir, grand fir, and western larch (Dewey and Jenkins 1979). Damage to cone crops has also been reported for western larch by Fellin and Shearer (1968) and for Douglas-fir by Chrisman et al. (1983).

Feeding by western spruce budworm on cone and seeds also reduces the probability of natural stocking of regeneration by about 30 percent, if harvesting is carried out during an outbreak (Carlson et al. 1982).[2] Larvae feed on and damage established conifer seedlings, but Carlson et al. (1983) indicated that in the western United States, feeding is not that severe on seedlings in managed stands regenerated through proper silvicultural methods. Unfortunately, the effects of various silvicultural treatments on vulnerability of stands and regeneration to budworm damage are not well quantified, and most silvicultural recommendations are based on qualitative information or intuition (Blum and MacLean 1984).

Damage to reproduction is directly related to the degree of infestation in the main stand. In a study of stands in northwestern New Brunswick, fir reproduction <0.3 m (1 ft) high suffered little damage, while 0, 3, 8, and 60 percent of living stems >0.3 m (1 ft) tall in the four plots were more than 95 percent defoliated (Vincent 1956). In the most severely defoliated plot, 2 and 44 percent of spruce and fir seedlings <0.3 m(1 ft) and 0.3–3.0 m (1-10 ft) tall were killed by budworm defoliation (Vincent 1956).

In general, it would appear that mortality of seedlings caused by defoliation is considerably less than mortality of mature trees, and in certain stand types in eastern North America, budworm outbreaks may actually result in a successional sequence of fir replacing fir (Baskerville 1975; MacLean 1984b). Regional differences do occur, however, and the long-term fate of other stand types, such as fir-spruce, fir-hardwood, or mixtures of spruce is less well understood and requires further study.

Effects of spruce budworm outbreaks on regeneration and long-term successional trends were examined in Ontario and Quebec by Ghent and coworkers (Ghent et al. 1957; Ghent 1958) and in Minnesota by Batzer and Popp (1985). Ghent et al. (1957) noted a 20 to 65 percent decrease in balsam fir seedling numbers over a 5-year period, and attributed 72 percent of this decrease to coverage by wind-broken, budworm-killed trees, and a further 16 percent of the decrease to severe shrub competition. This emphasizes that budworm outbreaks can have substantial indirect effects on regeneration, in addition to the results of direct feeding on seedlings. Ghent et al. (1957) further noted that trends in forest succession after budworm outbreaks were strongly dependent upon the region in which the data were gathered. Batzer and Popp (1985) in 1979 remeasured 24 spruce-fir stands in Minnesota that were devastated by spruce budworm from 1956 to 1963. They found that composition of the overstory changed from an average of 79 percent of the basal area in host species to 33 percent, but that the understory had minimally acceptable stocking of balsam fir in two-thirds of the stands. Other studies of effects of budworm outbreaks on regeneration and succession are currently under way in eastern Canada (e.g., Meades and Schooley 1981; MacLean 1984b; M. Huot, Marit. For. Res. Cent., Fredericton, N.B., personal communication) and the western United States (R.H. Ferguson and A. Stage, unpublished data).

The Use of Budworm Impact Data in Timber Supply Analysis and Vulnerability Rating

One of the major thrusts of budworm impact research during the CANUSA Program has been to provide data for forest management planning and the design of protection programs. This means incorporating data on growth loss and mortality caused by budworm into forest yield projections or timber supply analyses. The topic of forecasting growth and yield of budworm infested forests is reviewed in detail by Seymour (1985), and Crookston (1985). In this section, I will briefly discuss several points about using budworm impact research data in projecting effects of budworm outbreaks on timber supply, and highlight several recent developments in this area which are ongoing in New Brunswick.

Recent work in several regions has developed frameworks for including budworm effects in timber supply analyses (Crookston 1985; Seymour 1985). MacLean and Erdle (1984) described such a method for New Brunswick, in which an existing timber supply model (WOSFOP) (Hall 1978) was modified so that reductions in periodic growth rates and increases in periodic mortality caused by budworm defoliation could be included in yield projections. This allows data on growth loss and mortality from specific budworm research studies to be used directly in timber supply analysis for actual forest areas. Somewhat similar methods were used to incorporate budworm into spruce/fir wood supply/demand analyses for Maine (Sewall Co. 1983). The general methodology used in both of these studies includes an overall synthesis of effects of a specific budworm outbreak or defoliation scenario on periodic growth and mortality for specific stand types, essentially on the basis of all the data reviewed in this paper. The specific growth loss and mortality values used in several analyses are summarized in Table 4 for both protected and unprotected stand types. Analysis of projected yields from spruce-fir forests in New Brunswick over a 60-year time horizon using this method indicated that if protection were to cease, maximum sustainable harvest would be reduced by 23 to 36 percent under moderate budworm outbreak conditions and by 46 to 64 percent under severe outbreak conditions (MacLean and Erdle 1984).

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[2] Carlson, C.E., L.J. Theroux, and W.W. McCaughey, 1982. The influence of silvicultural practices on the susceptibility and vulnerability of northern Rocky Mountain forests to the western spruce budworm. U.S. For. Serv., Intermountain For. Range Exp. Stn., Ogden, UT. Unpub. Prog. Rep.

Table 4

Level of growth loss and mortality caused by budworm outbreaks, as used in several recent timber supply analyses. These values have been synthesized from the research literature, survey and inventory data, and assumptions about the magnitude of effects in specific stand types

Reference	Region	Stand type	Protection regime	Growth loss (%)[1]		Mortality (%)[2]	
				Immature[3]	Mature[3]	Immature[3]	Mature[3]
MacLean and Erdle 1984	New Brunswick	Spruce-fir	Protected	13	30	0	10
			Unprotected	39	47	30	50
Sewall Co. 1983	Maine	Spruce	Protected	32	32	0	0
			Unprotected	48	48	10-21	18-40
		Balsam fir	Protected	42	42	0	0
			Unprotected	79	79	57	70
Erdle et al. unpublished manuscript	New Brunswick	Balsam fir	Unprotected	60	70	50	70
		White/red spruce	Unprotected	40	50	30	50
		Black spruce	Unprotected	20	30	10	30

[1] Growth loss is the mean increment reduction during a 10-year outbreak for MacLean and Erdle (1984) and Erdle et al. (unpublished manuscript), and annual increment reduction in Sewall Co. (1983).

[2] Mortality is the total (cumulative) mortality for a 10-year outbreak (MacLean and Erdle 1984; Erdle et al. unpublished manuscript) and for a 6-year period (Sewall Co. 1983). Sewall Co. (1983) assumed that no budworm-caused mortality occurs in protected stands; the range of values presented for unprotected spruce refer to losses in mixedwood and softwood stand types.

[3] Immature stands specified as <60 years old in MacLean and Erdle (1984) and Erdle et al. (unpublished manuscript), and <40 years in Sewall Co. (1983).

One factor that has significantly affected the possibilities of using budworm impact data in forest management planning is the advent and increased usage of computer-based Geographic Information Systems (Erdle and Jordan 1984). These systems have been acquired and are in use by provincial or state and industrial agencies in several regions (e.g., British Columbia, New Brunswick, Maine). Geographic Information Systems store both descriptive data such as species composition, maturity, volume, and area of individual stands, and spatial data that uniquely define each stand's location in the forest (Erdle and Jordan 1984). Thus, with the aid of electronic plotting equipment, maps can be generated based on any specified theme residing in the descriptive data.

This capability of the Geographic Information System has been used to develop a stand harvest scheduling/vulnerability rating system in New Brunswick (Erdle et al., unpublished manuscript),[3] which quantifies stand vulnerability in terms of expected volume losses during a spruce budworm outbreak. In this system, two future yield projections are calculated for each stand in a management area, which represent protected (budworm spraying) and uncontrolled budworm outbreak (growth loss and mortality) situations. These two yield projections are then compared, and vulnerability is calculated as the difference in yield (cubic metres per hectare) between the protected and budworm-influenced stand projections at a given time. A harvest schedule for stands in the management area is determined as a function of both losses of yield due to stand overmaturity, and vulnerability. The method couples the New Brunswick Department of Natural Resources Geographic Information System, a wood supply model, and a simple stand development model to derive and produce a harvest schedule map that is compatible with a chosen harvest level (based on sustainable yield). The computing power of the Geographic Information System enables application of the technique to forest holdings of 100 000 ha (247,000 acres) or more (Erdle et al., unpublished manuscript).[3]

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[3] Erdle, T.A., D.A. MacLean, and E.C. Wang. An approach to integrating stand harvest scheduling, forest protection, and budworm vulnerability rating in New Brunswick. Unpublished manuscript.

The procedure for establishing vulnerability to budworm is as follows.

First, forest structure and stand yield data are compiled for the area of interest. This includes determining the spruce and fir proportions and age structure of each stand in the management area (e.g., proportions of immature, mature, and overmature spruce and fir). Second, the development of each stand is then projected for a 30-year period, assuming a continued protection program (control conditions), based on user-specified yield curves for different stand types and different spruce-fir components. Third, the development of each stand is projected assuming a budworm outbreak and no protection, based on explicitly defined levels of growth loss and mortality for specified budworm outbreaks or defoliation conditions. These projections use the methodology outlined in MacLean and Erdle (1984); differing growth loss and mortality levels are applied to balsam fir and spruce in immature and mature stands. Fourth, the vulnerability to budworm is calculated for each stand as the difference between the yields of the control stand projection and the budworm yield projection. Note that in this system, vulnerability of a specific stand is not constant but varies with stand development and the level of budworm damage. Lastly, all stands in the management area are ranked with respect to 1) the level of vulnerability, and 2) the rate of natural deterioration due to overmaturity, or 5-year volume losses (cubic metres per hectare) under control conditions. These rankings are then used to derive the harvest schedule for individual stands, i.e., which stands should be harvested in the 0-5 year period, 5-10 year period, etc.

The approach of using stand yield projections to rate vulnerability of individual stands appears to have considerable potential as a management tool. This method will allow managers to combine harvest scheduling, vulnerability rating, and protection (spray) planning into an integrated forest management system (Erdle et al., unpublished manuscript).[3] Protection can then be directed to where it is most needed and not wasted on stands scheduled for harvest in the near future. Similarly, stands that are most vulnerable or most severely damaged can be identified and harvested first to limit losses and to obviate protection measures. Perhaps most importantly, both vulnerability to budworm and results of protection activities can be evaluated in terms of expected stand yields and timber supply.

Discussion and Conclusions

This review shows that many scientific papers and reports have considered the effects of budworms on the forest. Over 150 references are cited in this paper, and I think it is significant that about three-quarters of these were published since 1978, the start of the CANUSA Program. This is strictly a correlation and cannot be interpreted as cause and effect (some of the work was not supported by CANUSA), but it is significant, nonetheless. I do not intend to review CANUSA studies of effects of spruce budworm outbreaks on forest growth and yield per se, but it is clear that relationships between defoliation and growth and yield are much better quantified now than they were in the mid-1970s. Also several noteworthy studies that will add to our knowledge are not yet complete.

In spite of its length and the large number of references cited, this review is by no means complete. Certain areas have been emphasized at the expense of others, and some effects of spruce budworm outbreaks have been omitted entirely, for example, degradation and loss of wood fiber in budworm-killed timber (see recent review by Basham [1984]), problems in salvaging timber affected by budworm (see Sewell and Maranda 1978), predisposition of budworm-damaged stands to attacks of other insects or diseases, or changes in ecosystem structure and functioning (e.g., nutrient cycling, energy flow, decomposition processes) resulting from budworm outbreaks. Other areas such as effects of budworm outbreaks on regeneration and succession, or predicting the risk of damage with hazard and vulnerability rating systems, have been discussed to some extent, but much additional information is available in other publications.

This review has shown that there are some clear differences in effects of budworm outbreaks in eastern and western North America. Outbreaks are more severe in the east. Complete mortality of stands, or widespread mortality over large areas, are common in unprotected eastern forests, but in the west, tree mortality generally appears to be relatively low or restricted to suppressed or intermediate crown classes of trees. Differences in effects of outbreaks among tree species and age classes of stands occur in both areas. Clearly effects of outbreaks are dependent primarily on the severity and duration of larval feeding (defoliation). The degree of loss of annual increment, therefore, varies considerably as an outbreak progresses and among different outbreaks. Growth losses and yield reduction appear also to be generally higher in eastern forests than in the west. Height growth losses, top-killing, and defect formation are much more important in timber used for sawlogs than for pulpwood, and these probably represent some of the most significant effects of budworm outbreaks in western forests.

In addition to differences in effects of budworm outbreaks between west and east, regional differences exist with respect to budworm outbreak dynamics, damage, and the forest resource (both composition and usage). The budworm may react differently in different "zones of abundance" (Hardy et al. 1983); and forest types, markets, and degree of usage vary considerably among regions. This was brought out in comparing studies of tree mortality caused by budworm in areas from Newfoundland to Ontario and the Lake States: the budworm is more of a problem in some areas than others. Therefore, forest management and protection strategies also differ among regions. The characteristics of the forest, available timber supply, and degree of industrial utilization determine the need for protection in terms of maintaining the required wood supply. That is, if large proportions of the forest are mature and vulnerable, and this constitutes the only available wood supply for the next two to three decades, there is no alternative but to protect, if industrial capacity is to be maintained.

Reviews conventionally end with a discussion of additional data needed. However, rather than just a plea for more data on effects of budworm outbreaks on forests, I feel that data are needed in some specific areas. As stated at the outset, this paper is slanted towards projection of effects of outbreaks on stand yield and timber supply for forest management and protection planning purposes. Therefore, information on periodic increment and mortality, and reduction of increment and mortality caused by specific outbreak/defoliation levels should be at the stand level, in terms of cubic metres per hectare. Management agencies and industrial users generally have yield projection or supply analysis systems in place, so data on deviation from expected yield (i.e., losses) for specific defoliation/stand type scenarios are often most useful. Significantly, more of this type of data is being gathered in recent years by provincial, state, or industrial agencies, from inventory permanent sampling plots. This reflects the (relatively) recent realization that timber supplies in many regions are not quite as rosy as once thought. A tight balance between demand and supply increases the importance of accurate yield projections.

In terms of more specific information requirements, in the east, more data are needed on mortality/growth loss/stand yields in immature stands, spruce species, and protected stands. Yield projections made for young stands are very important in determining sustainable harvest because of the current preponderance of mature and overmature age classes of forest in many regions that will be harvestable only for a finite length of time. Supply projections often depend upon substantial yields being harvestable from young stands at a specific future date; errors in these projections, or failure to account for yield reductions caused by budworm, could seriously alter sustainable harvest calculations. Additional information on effects of budworm on spruce species and protected stands are needed simply because very few data are currently available. Most protection programs are designed primarily to limit tree mortality; how much growth loss and yield reduction are occurring in these stands? Are these losses acceptable in managed young stands, or are alternative protection strategies warranted? How much defoliation can be tolerated and still have stands meet specific yield targets?

Many of the eastern data requirements also apply in the west. More data are required on stand yield reductions caused by budworm outbreaks, and particularly, on losses in product quality in sawlog material resulting from top-killing, defect formation, and decay. Emphasis should be on yield projections with and without budworm, and increased use of timber supply models for loss and hazard determination and policy analysis. Data requirements for projecting yield in budworm-infested forests in the west are discussed by Crookston (1985).

In stressing effects of budworm defoliation on forest growth and yield in this review, I have neglected another area in which data are badly needed. This concerns defoliator–host interactions: the reciprocal feedback effects of budworm defoliation on the forest and vice versa. Effects of stand structure, foliage chemistry or "quality" (see Fleming 1983), host species characteristics, and site conditions on budworm population dynamics, and effects of defoliation on tree or stand structure/functioning and thereby on future generations, are poorly understood. Yet determining the biological mechanisms which drive budworm/forest dynamics is really a prerequisite for dynamic mechanistic modeling or "understanding" the budworm/forest system. For instance, the harvest scheduling/vulnerability rating management procedure discussed in the last section ignores feedbacks between the forest and budworm dynamics, and thus conceivably could result in a suboptimal long-term course for the system. One reason for the dearth of information on budworm/forest feedback effects is that even in recent detailed work, budworm population dynamics and impact of defoliation on tree growth and mortality have largely been studied independently. Data are needed on changes in population dynamics occurring with, or as a result of, damage to the forest. Process-level experimental studies are also required, to determine the influence of changes in specific host parameters (e.g., stand structure, foliage quality) on budworm population dynamics. Attention is due to the feedbacks whereby current effects on the forest affect future budworm generations which subsequently have further effects on the forest, etc.

In conclusion I would like to emphasize again the importance of the acquisition and usage of computer-based Geographic Information Systems by industrial and provincial/state forest managers. Forest inventories are taking on a spatial dimension not previously available, and data manipulation or map generation only dreamed of in the past are now possible in many areas. These are the data management systems of the future; computers currently make it possible to consider and manipulate the data from each of 10,000 individual stands in a management area in formulating a management or protection plan, and to retain the spatial location of each stand in the forest.

There is much potential for research to make a significant contribution to forest management planning, both in terms of effects of budworm on growth and yield, and in many other areas, if scientists are willing to consider the needs of, and work with, forest managers. Baskerville (1983)[4] stated that up to the present, scientists have not done a good job of providing usable scientific information regarding budworm-forest management to policy makers and decision makers, part of the problem being that science is disciplinary, while management is multidisciplinary. If a portion of the scientific community was to concentrate on providing information usable in management decision making, they would be rewarded "by seeing a major impact of their work on what actually happens on-the-ground out there in the forest" (Baskerville 1983).[4]

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Literature Cited

Alfaro, R.I.; Shore, T.L.; Wegwitz, E. 1984. Defoliation and mortality caused by western spruce budworm: variability in a Douglas fir stand. J. Entomol. Soc. B.C. 81:33-38.

Alfaro, R.I.; Thomson, A.J.; Van Sickle, G.A. 1985. Quantification of Douglas-fir growth losses caused by western spruce budworm defoliation using stem analysis. Can. J. For. Res. 15:5-9.

Alfaro, R.I.; Van Sickle, G.A.; Thomson, A.J.; Wegwitz, E. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Can. J. For. Res. 12:780-787.

Archambault, L. 1983. Impact of defoliation caused by the spruce budworm on volume growth in three fir stands. Can. For. Serv., Ottawa. Res. Notes 3:17-19.

Bailey, R.E. 1982. The current status of the softwood resource on Cape Breton Island. N.S. Dep. Lands Forests, Truro, N.S. For. Res. Note No. 3.

Basham, J.T. 1984. Degradation and loss of wood fibre in spruce budworm-killed timber, and effects on utilization. For. Chron. 60:10-14.

Baskerville, G.L. 1975. Spruce budworm: super silviculturist. For. Chron. 51:138-140.

Baskerville, G.L. 1976. Report of the task force for evaluation of budworm control alternatives. Prepared for New Brunswick Cabinet Committee on Economic Development. New Brunswick Dep. Nat. Resour., Fredericton, N.B.

Baskerville, G.L. 1982. The spruce/fir wood supply in New Brunswick. For. Manage. Br., New Brunswick Dep. Nat. Resour., Fredericton, N.B. Rep. No. 0-88838-408-4.

Baskerville, G.L.; MacLean, D.A. 1979. Budworm-caused mortality and 20-year recovery in immature balsam fir stands. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-102.

Batzer, H.O. 1973a. Defoliation by the spruce budworm stimulates epicormic shoots on balsam fir. Environ. Entomol. 2:727-728.

Batzer, H.O. 1973b. Net effect of spruce budworm defoliation on mortality and growth of balsam fir. J. For. 71:34-37.

Batzer, H.O.; Bean, J.L. 1962. Spruce budworm defoliation causes continued top-killing and tree mortality in northeastern Minnesota. U.S. Dep. Agric., For. Serv., Lake States For. Exp. Stn., St. Paul, MN, Tech. Note No. 621.

Batzer, H.O.; Hastings, A.R. 1981. Rating spruce-fir stands for spruce budworm vulnerability in Minnesota. Pages 105-108 *in* Hazard rating systems in forest insect pest management. U.S. Dep. Agric., For. Serv., Washington, D.C. Gen. Tech. Rep. WO-27.

Batzer, H.O.; Popp, M.P. 1985. Forest succession following a spruce budworm outbreak in Minnesota. For. Chron. 61:75-80.

Beaulieu, J.; Hardy, Y.J. 1982. Mortalité du sapin baumier défolié par la tordeuse des bourgeons de l'épinette dans la région de la Gatineau au Québec. For. Chron. 58:213-219.

Belyea, R.M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part II. An assessment of the role of associated insect species in the death of severely weakened trees. J. For. 50:729-738.

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[4] Baskerville, G.L. 1983. Integrated pest management — myth or reality? Paper presented at Eastern Spruce Budworm Research Work Conf., Jan. 10-11, 1983. Orono, ME.

Bennett, D. 1978. Biological evaluation, western spruce budworm impact evaluation on the Bridger-Teton National Forest, 1976-77. U.S. Dep. Agric., For. Serv., Div. State Private For., Ogden, UT. Rep. 78-6.

Beveridge, R.L.; Cahill, D.B. 1984. Western spruce budworm feeding effects on conifers located on the Boise and Payette National Forests. U.S. Dep. Agric., For. Serv., Div. State Private For., Boise, ID. Rep. 84-7.

Bible, T. 1985. Economic considerations for spruce budworm management in North America. Pages 176-187 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Blais, J.R. 1958. The vulnerability of balsam fir to spruce budworm attack in northern Ontario, with special reference to the physiological age of the tree. For. Chron. 34:405-422.

Blais, J.R. 1962. Collection and analysis of radial growth data from trees for evidence of past spruce budworm outbreaks. For. Chron. 38:474-484.

Blais, J.R. 1964. Account of a recent spruce budworm outbreak in the Laurentide Park region of Quebec and measures for reducing damage in future outbreaks. For. Chron. 40:313-323.

Blais, J.R. 1965. Spruce budworm outbreaks in the past three centuries in the Laurentide Park, Quebec. For. Sci. 11:130-138.

Blais, J.R. 1968. Regional variation in susceptibility of eastern North American forests to budworm attack based on history of outbreaks. For. Chron. 44:17-23.

Blais, J.R. 1981. Mortality of balsam fir and white spruce following a spruce budworm outbreak in the Ottawa River watershed in Quebec. Can. J. For. Res. 11:620-629.

Blais, J.R. 1983a. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13:539-547.

Blais, J.R. 1983b. Predicting tree mortality induced by spruce budworm: a discussion. For. Chron. 59:294-297.

Blais, J.R.; Archambault, L. 1982. Rating vulnerability of balsam fir to spruce budworm attack in Quebec. Can. For. Serv., Laurentian For. Res. Cent., Ste. Foy, Quebec. Inf. Rep. LAU-X-51.

Blais, J.R.; Kettela, E.G.; Moody, B.H. 1981. History of spruce budworm outbreaks in eastern North America with special reference to Newfoundland. Pages 12-17 *in* J. Hudak and A.G. Raske, eds. Review of the spruce budworm outbreak in Newfoundland — its control and forest management implications. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. Inf. Rep. N-X-205.

Blum, B.M.; MacLean, D.A. 1984. Silviculture, forest management, and the spruce budworm. Chapter 6, Pages 83-102 *in* D.M. Schmitt, D.G. Grimble, and J.L. Searcy, tech. coords. Managing the Spruce Budworm in Eastern North America. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. No. 620.

Bousfield, W.E. 1979. Progress report on spruce budworm damage in Idaho and Montana, 1978. U.S. Dep. Agric., For. Serv., Div. State Private For., Missoula, MT. For. Insect Disease Manage. Rep. No. 79-11.

Bousfield, W.E. 1980. The effects of height growth loss on stands damaged by the western spruce budworm. U.S. Dep. Agric., For. Serv., North. Reg., Div. State Private For., Missoula, MT. For. Insect Disease Manage. Rep. No. 80-11.

Bousfield, W.E.; Frank, G.C. 1979. Remeasurement of western spruce budworm damage areas on the Clearwater National Forest, Idaho, 1978. U.S. Dep. Agric., For. Serv., Div. State Private For., Missoula, MT. For. Insect Disease Manage. Rep. No. 79-8.

Bousfield, W.E.; Williams, R. 1977. Impact of spruce budworm on the Nezperce National Forest, Idaho, 1976. U.S. Dep. Agric., For. Serv., Div. State Private For., Missoula, MT. For. Insect Disease Manage. Rep. No. 77-3.

Brann, T.B.; Reams, G.A.; Solomon, D.S. 1983. Spruce budworm growth impact study 1981 report. Coll. For. Resour., Univ. Maine, Orono, ME. Coop. For. Res. Unit, Res. Note No. 11.

British Columbia Ministry Forests. 1980. Forest and range resource analysis technical report. B.C. Min. For., Victoria, B.C. 802 p.

Brubaker, L.B.; Greene, S.K. 1979. Differential effects of Douglas-fir tussock moth and western spruce budworm defoliation on radial growth of grand fir and Douglas-fir. Can. J. For. Res. 9:95-105.

Canadian Forestry Service. 1979. Report of the Task Force for the review of the Canadian Forestry Service Research Program on the eastern spruce budworm. Can. For. Serv., Ottawa, Ont.

Canadian Forestry Service. 1982. Guidelines for predicting tree mortality caused by the spruce budworm, and measures for reducing losses. Can. For. Serv., Ottawa, Ont. Special Folder.

Carlson, C.E.; McCaughey, W.W. 1982. Indexing western spruce budworm activity through radial increment analysis. U.S. Dep. Agric., For. Serv., Intermountain For. Range Exp. Stn., Ogden, UT. Res. Pap. INT-291.

Carlson, C.E.; Fellin, D.G.; Schmidt, W.C. 1983. The western spruce budworm in northern Rocky Mountain forests: a review of ecology, insecticidal treatments and silvicultural practices. Pages 76-103 *in* J. O'Loughlin and R.D. Pfister, eds. Management of Second-Growth Forests: The State of Knowledge and Research Needs. Montana For. Conserv. Exp. Stn., Univ. Montana, Missoula, MT.

Chrisman, A.B ; Blake, G.M.; Shearer, R.C. 1983. Effects of western spruce budworm on Douglas-fir cone production in western Montana. U.S. Dep. Agric., For. Serv., Intermountain For. Range Exp. Stn., Ogden, UT. Res. Pap. INT-308.

Clowater, W.G.; Andrews, P.W. 1981. An assessment of damage caused by the spruce budworm on spruce and balsam fir trees in New Brunswick. For. Manage. Br., New Brunswick Dep. Nat. Resour., Fredericton, N.B. Rep. No. 0-88838-087-9.

Collis, D.G.; Van Sickle, G.A. 1978. Damage appraisal cruises in spruce budworm defoliated stands of Douglas-fir in 1977. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Pest Rep. BC-P-19.

Corcoran, D.J. 1980. The impact of spruce budworm on management at Great Northern Paper Co. Maine For. Rev. 13 (summer 1980):10-11.

Craighead, F.C. 1924. Studies on the spruce budworm (*Cacoecia fumiferana* (Clem.)). Part II. General bionomics and possibilities of prevention and control. Can. Dep. Agric., Ottawa, Ont. Tech. Bull. No. 37 (n.s.). pp. 28-91.

Craighead, F.C. 1925. Relation between mortality of trees attacked by the spruce budworm (*Cacoecia fumiferana* Clem.) and previous growth. J. Agric. Res. 30:541-555.

Crookston, N.L. 1985. Forecasting growth and yield of budworm infested forests. Part II: Western North America and Summary. Pages 214-230 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworm research. Proc. CANUSA Spruce Budworms Research Symp. 16-20, Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Devine, M.E.; Trial, H. Jr. 1980. Maine spruce budworm mortality studies and future plans. Maine For. Rev. 13 (summer 1980): 11-16.

Dewey, J.E. 1970. Damage to Douglas-fir cones by *Choristoneura occidentalis*. J. Econ. Entomol. 63:1804-1806.

Dewey, J.E.; Jenkins, M.J. 1979. An evaluation of cone and seed insects in selected seed production areas in Region 1. U.S. Dept. Agric., For. Serv., Div. State Private For., Missoula, MT. Rep. No. 79-16.

Duff, G.H.; Nolan, N.J. 1953. Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in *Pinus resinosa* Ait. Can. J. Bot. 31:471-513.

Duff, G.H.; Nolan, N.J. 1957. Growth and morphogenesis in the Canadian forest species. II. Specific increments and their relation to the quantity and activity of growth in *Pinus resinosa* Ait. Can. J. Bot. 35:527-572.

Erdle, T.; Jordan, G. 1984. Computer-based mapping in forestry: a view from New Brunswick. Can. For. Industries 104: 38-46.

Fayle, D.C.F. 1973. Patterns of annual xylem increment integrated by contour presentation. Can. J. For. Res. 3:105-111.

Fayle, D.C.F.; MacIver, D.; Bentley, C.V. 1983. Computer-graphing of annual ring widths during measurement. For. Chron. 59:291-293.

Fellin, D.G.; Shearer, R.C. 1968. Spruce budworm larvae damage western larch cones and seeds. J. For. 66:568-570.

Fellin, D.G.; Shearer, R.C.; Carlson, C.E. 1983. Western spruce budworm in the northern Rocky Mountains. Western Wildlands 9(1):2-7.

Ferrell, G.T.; Scharpf, R.F. 1982. Stem volume losses in grand firs topkilled by western spruce budworm in Idaho. U.S. Dep. Agric., For. Serv., Pac. Southwest For. Range Exp. Stn., Berkeley, CA. Res. Pap. PSW-164.

Ferguson, R.H.; Kingsley, N.P. 1972. The timber resources of Maine. U.S. Dep. Agric., For. Serv., Northeast For. Exp. Stn., Broomall, PA. Resour. Bull. NE-26.

Fettes, J.J. 1950. Investigations of sampling techniques for population studies of the spruce budworm on balsam fir in Ontario. Can. For. Serv., Forest Insect Lab., Sault Ste. Marie, Ont. Ann. Tech. Rep. 4:163-401.

Fleming, R.A. 1983. Foliage quality and its effect on budworm populations: a modeller's viewpoint. Pages 113-123 *in* R.L. Talerico and M. Montgomery, tech. coords. Proc. Forest Defoliator — Host Interactions: A Comparison Between Gypsy Moth and Spruce Budworms. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Stn., Broomall, PA. Gen. Tech. Rep. NE-85.

Fowler, G.W.; Witter, J.A. 1982. Accuracy and precision of insect density and impact estimates. Great Lakes Entomol. 15:103-117.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, New York.

Gasson, R.; Noble, T.E. 1983. Identify potential losses to mortality. Can. For. Industries 103(12):19-23.

Ghent, A.W. 1958. Studies of regeneration in forest stands devastated by the spruce budworm. II. Age, height growth and related studies of balsam fir seedlings. For. Sci. 4:135-146.

Ghent, A.W.; Fraser, D.A.; Thomas, J.B. 1957. Studies of regeneration in forest stands devastated by the spruce budworm. I. Evidence of trends in forest succession during the first decade following budworm devastation. For. Sci. 3:184-208.

Hall, T.H. 1978. Toward a framework for forest management decision-making in New Brunswick. New Brunswick Dep. Nat. Resour., Fredericton, N.B. Rep. No. TR1-78.

Hall, T.H. 1981. Forest management decision-making: art or science. For. Chron. 57:233-238.

Hardy, Y.J.; Lafond, A.; Hamel, L. 1983. The epidemiology of the current spruce budworm outbreak in Quebec. For. Sci. 29:715-725.

Harris, J.W.E.; Alfaro, R.I.; Dawson, A.F.; Brown, R.G. 1985. The western spruce budworm in British Columbia 1909-1983. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Inf. Rep. BC-X-257.

Howse, G.M.; Harnden, A.A.; Meating, J.H.; Carrow, J.R. 1982. The 1980 spruce budworm situation in Ontario. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. Inf. Rep. O-X-336.

Hudak, J.; Raske, A.G., eds. 1981. Review of the spruce budworm outbreak in Newfoundland — its control and forest management implications. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. Inf. Rep. N-X-205.

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of the western spruce budworm in the American northern Rocky Mountain area from 1922 through 1971. U.S. Dep. Agric., For. Serv., Intermountain For. Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-20.

Jordan, G.A.; Ballance, R.H. 1983. A microcomputer-based annual ring measurement system. For. Chron. 59:21-25.

Karpinski, C. Jr.; Witter, J.A. 1982. Plot size and number of plots needed to assess spruce budworm impact. Can. J. For. Res. 12:332-336.

Kettela, E.G. 1983. A cartographic history of spruce budworm defoliation 1967 to 1981 in eastern North America. Can. For. Serv., Ottawa, Ont. Inf. Rep. DPC-X-14.

Kleinschmidt, S.M.; Baskerville, G.L.; Solomon, D.S. 1980a. Foliage weight distribution in the upper crown of balsam fir. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Stn., Broomall, PA. Res. Pap. NE-455.

Kleinschmidt, S.M.; Baskerville, G.L.; Solomon, D.S. 1980b. Reduction of volume increment in fir-spruce stands due to defoliation by spruce budworm. Faculty For., Univ. New Brunswick, Fredericton, N.B. Res. Pap.

Kulman, H.M. 1971. Effects of insect defoliation on growth and mortality of trees. Annu. Rev. Entomol. 16:289-325.

Lynch, A.M.; Witter, J.A. 1985. Relationships between balsam fir mortality caused by the spruce budworm and stand, site and soil variables in Michigan's Upper Peninsula. Can. J. For. Res. 15:141-147.

Lynch, A.M.; Fowler, G.W.; Witter, J.A. 1984. Development of empirical models to rate spruce-fir stands in Michigan's Upper Peninsula for hazard from the spruce budworm (Lepidoptera: Tortricidae): a case history. Great Lakes Entomol. 17:163-174.

Lynch, A.M.; Witter, J.A.; Olson, C.E. Jr. 1984. Spruce budworm hazard-rating systems in the Lake States. Pages 62-68 *in* D.P. Ostaff, M.D. Cameron, and E.J. Mullins, eds. Proc. Damage Assessment Working Group, CANUSA Spruce Budworms Program. 25-26, Oct. 1983, Bangor, ME. Can. For. Serv., Ottawa, Ont.

MacLean, D.A. 1979. Spruce budworm-caused balsam fir mortality on the Cape Breton Highlands 1974-1978. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-97.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56:213-221.

MacLean, D.A. 1981. Impact of defoliation by spruce budworm populations on radial and volume growth of balsam fir: a review of present knowledge. Mitt. Forstl. Bundes. Wien 142:293-306.

MacLean, D.A. 1982. Vulnerability rating of forests in New Brunswick and Nova Scotia to budworm attack. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-132.

MacLean, D.A. 1984a. Number of plots needed to estimate tree mortality caused by spruce budworm defoliation. Can. For. Serv. Ottawa. Res. Notes 4:2-3.

MacLean, D.A. 1984b. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. For. Chron. 60:273-279.

MacLean, D.A. 1985. Predicting the risk of spruce budworm damage using hazard and vulnerability rating systems. Pages 113-120 *In* Proc. Symp. Spruce-Fir Management and Spruce Budworm. SAF Region VI Tech. Conf., 24-26, April, 1984. Burlington, VT. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-99. 217 p.

MacLean, D.A.; Erdle, T.A. 1984. A method to determine effects of spruce budworm on stand yield and wood supply projections for New Brunswick. For. Chron. 60:167-173.

MacLean, D.A.; Lidstone, R.G. 1982. Defoliation by spruce budworm: estimation by ocular and shoot-count methods and variability among branches, trees, and stands. Can. J. For. Res. 12:582-594.

MacLean, D.A.; Ostaff, D.P. 1983. Sample size – precision relationships for use in estimating stand characteristics and spruce budworm caused tree mortality. Can. J. For. Res. 13:548-555.

MacLean, D.A.; Kline, A.W.; Lavigne, D.R. 1984. Effectiveness of spruce budworm spraying in New Brunswick in protecting the spruce component of spruce-fir stands. Can. J. For. Res. 14:163-176.

McLintock, T.F. 1955. How damage to balsam fir develops after a spruce budworm epidemic. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Stn., Orono, ME. Stn. Pap. No. 75.

Meades, W.J.; Schooley, H.O. 1981. Chap. V. Damage caused by the spruce budworm. 3. Damage by the present outbreak to the forests of Newfoundland to 1979. (a.) Commercial fibre production. (iii) Future stands. Pages 49-54 *in* J. Hudak and A.G. Raske, eds. Review of the spruce budworm outbreak in Newfoundland: its control and management implications. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. Inf. Rep. N-X-205.

Meating, J.H.; Lawrence, H.D.; Howse, G.M.; Carrow, J.R. 1982. The 1981 spruce budworm situation in Ontario. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. Inf. Rep. O-X-343.

Miller, C.A. 1977. The feeding impact of spruce budworm on balsam fir. Can. J. For. Res. 7:76-84.

Mlodziansky, A.K. 1898. Measuring the forest crop. U.S. Dep. Agric., Div. For., Washington, D.C. Bull. 20. 71 p.

Mog, T.P.; Witter, J.A. 1979. Field techniques for assessing the impact of the spruce budworm (Lepidoptera: Tortricidae) in Michigan's upper peninsula. Great Lakes Entomol. 12:213-218.

Mog, T.P.; Lynch, A.M.; Witter, J.A. 1982. Impact of the spruce budworm (Lepidoptera: Tortricidae) on the Ottawa and Hiawatha National Forests, 1978-1980. Great Lakes Entomol. 15:1-24.

Mott, D.G.; Nairn, L.D.; Cook, J.A. 1957. Radial growth in forest trees and effects of insect defoliation. For. Sci. 3:286-304.

New Brunswick Department of Natural Resources. 1981. New Brunswick Forest Inventory. New Brunswick Dep. Nat. Resour., For. Manage. Br., Fredericton, N.B. Rep. No. 0-88838-372-X.

Ostaff, D.P. 1980. Condition of balsam fir on research plots on Cape Breton Island in the fall of 1980. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Tech. Note No. 17.

Ostaff, D.P. 1982. Condition of balsam fir on research plots on Cape Breton Island ten years after the start of a spruce budworm outbreak. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Tech. Note No. 65.

Ostaff, D. 1983. A wood quality study of dead and dying balsam fir — the incidence of *Armillaria* root rot. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Tech. Note No. 82.

Ostaff, D.P.; Newell, W.R. 1981. Spruce mortality in Nova Scotia caused by the spruce beetle *Dendroctonus rufipennis* Kby. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-122.

Otvos, I.S.; Moody, B.H. 1978. The spruce budworm in Newfoundland: history, status, and control. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. Inf. Rep. N-X-150.

Patee, R.K. 1966. Spruce budworm damage survey by Division of Timber Management, Intermountain Region, 1965. U.S. Dep. Agric., For. Serv., Intermountain Region, Ogden, UT.

Pedersen, N.L. 1981. The effects of spruce budworm defoliation on growth characteristics of balsam fir. Sch. For., Lakehead Univ., Thunder Bay, Ont. BSF Thesis.

Pendrel, B.A. 1981. Condition of fir and spruce in forests of Cape Breton Island, Cumberland and Colchester counties — Nova Scotia, 1981. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Tech. Note No. 39.

Pendrel, B.A. 1982. Condition of forest stands on Cape Breton Island 1982 — An aerial view. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Tech. Note No. 64.

Piene, H. 1980. Effects of insect defoliation on growth and foliar nutrients of young balsam fir. For. Sci. 26:665-673.

Piene, H. 1981. Early growth responses to operational spacing in young balsam fir stands on the Cape Breton Highlands, Nova Scotia. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-125.

Piene, H. 1983. Nondestructive estimation of foliar biomass in balsam fir. Can. J. For. Res. 13:672-677.

Piene, H. 1984. Defoliation by the spruce budworm: growth loss and recovery of balsam fir trees. Pages 22-24 *in* D.P. Ostaff, M.D. Cameron, and E.J. Mullins, eds. Proc. Damage Assessment Working Group, CANUSA Spruce Budworms Program. 25-26, Oct. 1983, Bangor, ME. Can. For Serv., Ottawa, Ont.

Piene, H.; MacLean, D.A.; Wall, R.E. 1981. Effects of spruce budworm caused defolation on the growth of balsam fir: experimental design and methodology. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-128.

Powell, G.R. 1973. The spruce budworm and megasporangiate strobili of balsam fir. Can. J. For. Res. 3:424-429.

Raske, A.G. 1981. Chap. V. Damage caused by the spruce budworm. 1. Damage to trees. Pages 30-41 *in* J. Hudak and A.G. Raske, eds. Review of the spruce budworm outbreak in Newfoundland: its control and management implications. Can. For. Serv., Nfld. For. Res. Cent., St. John's. Nfld. Inf. Rep. N-X-205.

Raske, A.G. 1984. Analysis of budworm-caused tree mortality in Newfoundland. Pages 2-9 *in* D.P. Ostaff, M.D. Cameron, and E.J. Mullins, eds. Proc. Damage Assessment Working Group, CANUSA Spruce Budworms Program. 25-26, Oct. 1983, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Raske, A.G.; Rowe, J.D. 1982. Impact of the spruce budworm on some major forest types of Newfoundland. XVIII. Summary of 1981 data of spruce budworm impact plots. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. File Rep. Study 5281.

Raske, A.G.; Sutton, W.J. 1982. Maximum possible salvage of budworm-killed stands in Newfoundland and some economic consequences. Can. For. Serv., Ottawa. Res. Notes 2:25-26.

Raske, A.G.; Clarke, L.J.; Sutton, W.J. 1982. The status of the spruce budworm in Newfoundland in 1981. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. Inf. Rep. N-X-210.

Reed, F.L.C., and Associates Ltd. 1978. Forest management in Canada. Vol. 1. Can. For. Serv., Forest Mgmt. Inst., Ottawa, Ont. Inf. Rep. FMR-X-102.

Ross, D.A.; Van Sickle, G.A.; Fiddick, R.L.; Collis, D.G. 1978. Status of western spruce budworm on Douglas-fir in British Columbia. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C.

Salonius, P.O.; Fisher, R.A.; Mahendrappa, M.K. 1982. An alternative method of measuring fertilizer effects in forest stands. Can. J. For. Res. 12:146-150.

Sanders, C.J.; Carrow, J.R. (Cochairmen). 1983. The spruce budworm problem in Ontario — real or imaginary? Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. COJFRC Symp. Proc. O-P-11.

Schmiege, D.C. 1961. Mortality and top-killing of spruce-fir caused by repeated budworm defoliation. U.S. Dep. Agric., For. Serv., Lake States For. Exp. Stn., St. Paul, MN. Tech. Note No. 597.

Schmidt, W.C.; Fellin, D.G. 1973. Western spruce budworm damage affects form and height growth of western larch. Can. J. For. Res. 3:17-26.

Schooley, H.O. 1978. Effects of spruce budworm on cone production by balsam fir. For. Chron. 54:298-301.

Schooley, H.O. 1980. Damage to black spruce cone crops by the spruce budworm. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. Inf. Rep. N-X-187.

Seegrist, D.W.; Arner, S.L. 1982. Mortality of spruce and fir in Maine in 1976-78 due to the spruce budworm outbreak. U.S. Dep. Agric., For. Serv., Northeast For. Exp. Stn., Broomall, PA. Res. Pap. NE-491.

Sewell, C.D.; Maranda, J. 1978. Problems in salvaging timber affected by the spruce budworm. For. Eng. Res. Inst. Can., Pointe Claire, Que. Tech. Rep. TR-25.

Sewall, James W. Co. 1983. Spruce-fir wood supply/demand analysis. Final report to Maine Dep. Conserv. James W. Sewall Co., Old Town, ME.

Seymour, R.S. 1980. Vulnerability to spruce budworm damage and 100-year development of mixed red spruce-fir in north central Maine. Yale Univ., PhD Thesis.

Seymour, R.S. 1985. Forecasting growth and yield of budworm-infested forests. Part I: Eastern North America. Pages 200-213 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Shearer, R.C. 1980. Regeneration establishment in response to harvesting and residue management in a western larch – Douglas-fir forest. Pages 249-269 *in* Proc. Symp. Environmental Consequences of Timber Harvesting in Rocky Mountain Coniferous Forests. U.S. Dep. Agric., For. Serv., Intermountain For. Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-90.

Shepherd, R.; Harris, J.W.E.; Van Sickle, G.A.; Fiddick, L.; McMullen, L. 1977. Status of western spruce budworm on Douglas-fir in British Columbia. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C.

Silver, G.T. 1960. Notes on a spruce budworm infestation in British Columbia. For. Chron. 36:362-374.

Solomon, D.S. 1984. Foliage weight production and bole growth of balsam fir trees defoliated by the spruce budworm. Pages 25-34 *in* D.P. Ostaff, M.D. Cameron, and E.J. Mullins, eds. Proc. Damage Assessment Working Group, CANUSA Spruce Budworms Program, 25-26, Oct. 1983, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Stillwell, M.A. 1956. Pathological aspects of severe spruce budworm attack. For. Sci. 2:174-180.

Stocks, B.J. 1985. Budworm damage and fire hazard. Pages 188-199 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Swaine, J.M.; Craighead, F.C. 1924. Studies on the spruce budworm (*Cacoecia fumiferana* Clem.). Part I. A general account of the outbreaks, injury and associated insects. Can. Dep. Agric., Ottawa, Ont. Tech. Bull. 37 (n.s.). pp. 3-27.

Swetnam, T.W.; Thompson, M.A.; Sutherland, E.K. (In press). Measuring radial growth of defoliated trees using dendrochronology. U.S. Dept. Agric., For. Serv., Washington, D.C. Agric. Handb.

Thomson, A.J.; Van Sickle, G.A. 1980. Estimation of tree growth losses caused by pest activity. Can. J. For. Res. 10:176-182.

Thomson, A.J.; Alfaro, R.I.; Van Sickle, G.A. 1982. Evaluating effects of western spruce budworm on Douglas-fir volume growth. Can. For. Serv., Ottawa. Res. Notes 2:24-25.

Timmer, V.R.; Verch, B.R. 1983. SAPP: A computer program for plotting stem analysis. For. Chron. 59:298-303.

van der Beek, J.; Maessen, P.P. Th. M. 1981. The "Dorschkamp" equipment for measuring width of annual growth rings. Nederl. Bosb. Tijdschr. 53:158-164.

Van Sickle, G.A.; Alfaro, R.I.; Thomson, A.J. 1983. Douglas-fir height growth affected by western spruce budworm. Can. J. For. Res. 13:445-450.

Vincent, A.B. 1956. Balsam fir and white spruce reproduction on the Green River watershed. Can. Dep. North. Affairs Natural Resour., For. Res. Div., Ottawa, Ont. Tech. Note No. 40.

Wellings, F.R.; Bailey, R.E. 1982. Cumberland County budworm losses. Nova Scotia Dep. Lands Forests, Truro, N.S. For. Tech. Note No. 4.

Williams, C.B. Jr. 1967. Spruce budworm damage symptoms related to radial growth of grand fir, Douglas-fir, and Engelmann spruce. For. Sci. 13:274-285.

Witter, J.A.; Simmons, G.A.; Montgomery, B.A.; Rogan, R.G. 1982. Technology transfer in forest pest management: a case history. Great Lakes Entomol. 15:297-302.

Economic Considerations for Spruce Budworm Management in North America

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This review emphasizes nonbiomass impacts of budworm. There are three classes of physical budworm effects — mortality, growth loss, scenic impairment — and four classes of forest management objectives — public and private Canadian and United States forest lands. Impact of all kinds occurs across all tenures. Developing a single management response strategy is probably not possible — implementation of more than one plan within a region may be necessary. This paper places these and related issues into perspective and reviews some basic principles for economic-impact evaluation. Different problems and research approaches taken in eastern and western work, specific budworm impacts, evaluation methods and management responses and the effect of land tenure on feasible management options are discussed.

Cette communication porte sur les répercussions de la tordeuse sur d'autres éléments que la biomasse. La tordeuse exerce trois catégories d'effets physiques (mortalité, ralentissement de la croissance, enlaidissement des forêts), et on compte quatre catégories d'objectifs d'aménagement forestier (pour les forêts publiques et privées du Canada et des États-Unis). Tous les types de propriétés forestières subissent ces répercussions. Il est probablement impossible d'élaborer une seule stratégie d'aménagement; une même région peut nécessiter plusieurs plans. Cette communication a pour objet de situer ces questions et les questions connexes dans leur perspective et d'examiner certains principes de l'évaluation des répercussions économiques. Elle traite des différents problèmes et des voies adoptées par la recherche dans l'Est et dans l'Ouest, des répercussions spécifiques des tordeuses, des méthodes d'évaluation, des ripostes des aménagistes et des effets du régime foncier sur les options possibles de l'aménagement.

Introduction

The focus of this paper is on nonbiomass impacts of budworm, their evaluation, and selection of management options. Virtually all economic impacts, however, are directly linked to changes in stand volume attributable to budworm. Unless stated otherwise, the following discussion assumes that land managers had obtained estimates of stand-volume losses or of any other budworm-affected stand attribute before an economic analysis was undertaken. In the northeastern United States and Canada, those losses will usually be estimated from forest surveys. In the West, PROGNOSIS-SBW can be used for that purpose (Sheehan et al., in press).

Evaluating economic impacts of budworm in North America is complicated because the impacts are determined by interactions among the physical effects considered and the particular set of objectives important to managers. In North America, at least three classes of physical budworm effects and up to four classes of forest-management objectives are important, depending on land tenure. Physical effects would include mortality, growth loss, and scenic impairment. The tenures where those effects occur are public and private Canadian and United States forest lands.

Similar budworm impacts often occur on more than one tenure in the same geographic region. Heavy stand mortality, an important problem in the Northeast, and stand-growth losses, an important problem in the West, occur across all four tenures. A single management-response strategy for regional budworm problems is probably not possible because management objectives may differ in each region according to tenure, even when physical effects are the same. Implementing more than one management plan for the same budworm problem within a region may be necessary.

Furthermore, scenic impairment is important in the southwestern United States and parts of western Canada, because it may lead to economic losses for private enterprises that depend on recreation visits. These indirect economic losses that might be attributable to scenic impairment have not been extensively evaluated. They are considered in this paper to provide a complete discussion of the potential economic effects of budworm outbreaks.

The following section of this paper presents some basic principles for budworm economic-impact evaluations. Subsequent sections include discussions on: different problems and research approaches taken in the eastern and western components of CANUSA; merchantable yield effects, evaluation methods, management responses, local and regional effects, recreation/scenic effects, and the effect of land tenure on management options.

Basic Principles for Evaluating Socioeconomic Impact of Budworm

Understanding how a forest can be viewed as an economic asset is important to developing management strategy for budworm. Consider a forest as a set of harvestable volumes separated into an age-class distribution. In this simple view, each age class of tree species represents a separate asset in a portfolio. The assets have an expected maturity date defined by harvest. Assuming that wood prices can be forecast, each asset increases in value according to the rate merchantable volume is added to trees by biological growth. A forest then can be viewed as a portfolio containing a set of assets similar to conventional economic assets, each with an expected maturity date and perhaps different yield according to tree growth, species, and market value.

Forest-management plans are developed to establish financial plans that manage a forest portfolio by liquidating and introducing assets through harvesting and site regeneration. Crucial to plan development is knowledge about expected yields and maturity dates. Budworm outbreaks can change both. Extensive mortality in stands not scheduled for harvest requires salvage or abandonment, with the effect of truncating asset-maturity periods. Growth and yield losses reduce the effective financial yield of holding each asset. When budworm outbreaks affect an existing plan, the plan will, in general, be nonoptimal. Managers must then either redevelop plans according to new yield and maturity information or take action to re-establish existing plans.

Budworm outbreaks on forest lands can be considered as events that change or block desired forest-management outcomes. In addition, changed management plans can lead to further economic impacts in regions or localities that depend on forest outcomes, such as harvest or recreation opportunities.

Certain nomenclature conventions have led to some confusion between forest managers and economists evaluating budworm problems. Most prominent are the notions of cost, loss, and benefits of outbreaks and treatment. Understanding these terms is pivotal to developing appropriate cost-benefit analyses. When facing an outbreak, managers usually consider the costs of budworm as the projected losses that would occur in terms of preoutbreak management objectives. Those "losses" are then compared to the cost of treating an outbreak. Treating an outbreak is assumed to return forests to the preoutbreak management regime, offsetting losses. The net benefits of treatment are then the difference between the value that would be lost to budworm outbreaks on the acreage proposed for treatment, less treatment costs. When treatment costs are less than treatment benefits (net benefits are positive), treatment is usually justified on economic grounds.

In other cases, treatment may place forests into a new management regime different from preoutbreak patterns. Then the difference between the value of the preoutbreak regime and the new, postoutbreak treated regime — which may be positive or negative — must be added to the net benefits just described. If the resulting net benefits are positive, treatment is usually economically justified.

Implicit in the discussion are the specific management objectives for a forest or stand. When forests are in managed rotation to maximize harvest volume or value either as public or private lands, for example, budworm damage can be evaluated in terms of lost harvest volume, or the dollar value of that volume.

When forests are managed for other harvest and nonharvest objectives, evaluating budworm damages may not be quite so straightforward. For example, managers are often concerned with local and regional economic impacts related to harvest. Those might include local wood products employment or maintenance of a severance tax base for localities. Or managers may be concerned with nonharvest objectives, such as local recreation expenditures. When such off-forest effects are considered, managers should first consider how forest outcomes are linked to specific off-forest, local economic activities. Budworm impacts can then be traced through those linkages to identify local economic impacts. If known, the dollar value of off-forest effects should then be included in an economic analysis. Note that off-forest gains may also result from outbreaks.[1] The value of those effects — positive or negative — should be added to the net benefits of treatment.

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[1] Bible, T.D. 1983. Short run input substitution in natural resource dependent regions: empirical results and policy implications. Unpublished working paper on file at: Oregon State University, Department of Economics, Corvallis, OR.

In summary, evaluating budworm impacts is based on managers taking a series of interrelated steps: managers should determine how budworm will influence preoutbreak forest-management plans; next, they should determine the costs, or value losses associated with changed forest plans (those will usually be the treatment benefits); the costs of treating budworm and returning to preoutbreak or new, postbreak plans should be assessed; and the costs and benefits of treatment should be compared to determine whether treatment is economically justified.

Note carefully, however, that the management sequence outlined here is usually applied by assuming that budworm treatment will return expected forest outcomes to preoutbreak patterns. Recent research in the West, however, has explored the possibilities for treatment regimes that would place forests on new management regimes.[2] Special focus has been placed on treatment regimes that would reduce the probability of budworm outbreak in the future (Carlson et al. 1985; Blum 1985). If budworm treatment places forests into new regimes, any additional benefit of treatment in terms of the differences in value between new and old regimes must be considered.

Finally, note that treatment — as discussed in this paper — includes the entire range of chemical, silvicultural, harvest scheduling, and other budworm-management options available. Complete details are provided elsewhere in these proceedings.

The CANUSA Experience in Economic-Impact Evaluation and Modeling: Eastern and Western Components

Two distinct approaches have been taken for economic-impact modeling in the East and West. The approaches reflect several important aspects of budworm outbreaks that differ between the East and West. The budworm species are different, different tree species are affected, and different types of stand damage are important to managers. The two insect species are not a concern of this paper — nor are tree species a direct concern. The types of stand damage in each region — combined with certain biological aspects of the affected species — have influenced research on economic-impact evaluation. Those influences and the resulting recommendations for management personnel who will conduct economic analyses are the focus here. A full description of CANUSA-West's research efforts can be found in Brookes et al. (in press a, b, c).

In general, budworm damage consists of tree mortality and growth losses during and after an outbreak. The relative incidence of those effects is a principal difference between the East and West. In the East, heavy mortality is a major problem; in the West, however, growth and yield losses are the predominant issue.

Those differences affect managment's response to an outbreak. In the East, most of the economic impacts are felt in the near term. Mortality leads to net loss of timber (excluding salvage), and management action must be taken relatively quickly to offset those losses. The principal historical focus of Eastern analyses has been on estimating net loss of timber (excluding salvage) and evaluating treatment options in that context. Through CANUSA-East research, interest in budworm treatment has evolved toward developing management plans that treat current outbreaks while modifying forest-species composition to reduce the probability of budworm outbreaks in the future.

As a consequence, economic analyses for those problems have addressed issues related to current treatment benefits plus the future net benefits of altering stand composition and management regimes. Further, the focus has been on evaluating a set of predetermined management responses to budworm. Specifically, managed responses are developed according to biological or silvicultural criteria before they are evaluated for economic viability. Thus, a set of possible responses are "predetermined," before an economic assessment.

In the West, on the other hand, budworm outbreaks mostly affect tree yield and growth. Mortality, other than top-kill, is not as serious a problem as in the East. As a result, the economic impact of budworm is not immediate and may not be felt for decades, depending on expected harvest dates for affected stands.

Many management plans and options that would not be available in the East are open to Western managers. Accordingly, economic-impact research in the West has focused on developing optimal managed responses to budworm, rather than evaluating predetermined responses. Managed responses are developed while biological, silvicultural, and economic criteria are considered simultaneously. Detailed parameters of a response are usually unknown before an outbreak, but are developed to optimize managed forest objectives. The goal in the West has been — given a general management objective, such as maximizing harvest volume or value over time — to develop new management plans that meet the objective with budworm-affected yields. The new plans are then evaluated against the old plan, and value differences are compared to treatment costs.

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[2] Berck, P.; Bible, T.D. 1984. Forest wide economic interpretations of the allowable cut effect. 5 p. Unpublished paper on file at: Oregon State University, Department of Economics, Corvallis, OR.

The loss in an outbreak will be the difference between management plan values under pre- and postoutbreak yield assumptions. That loss, if positive, can be compared to treatment costs in the conventional manner.

Another important difference between budworm problems in the East and West relates to harvest volumes and timing. In the East, outbreaks usually increase current harvest potential through mortality salvage. An issue addressed by economic-impact analysis is whether sufficient productive capacity is available to process salvage. Otherwise, mortality salvage has no value and is lost. Another related issue is whether significant mortality occurring across age classes at the same time could lead to "pulse harvesting" (see Clark 1976). Although not explicitly addressed by the Eastern program, the possibility of short-term timber famines could increase future off-forest losses attributable to budworm.

In the West, outbreaks usually reduce future harvests through present growth and yield losses. An issue explicitly addressed by economic-impact analysis in the West is whether reductions in the future will lead to mill closures and local unemployment. Another issue is whether reduced harvests will affect local government operations through reductions in severance tax receipts. The difference in management strategies for dealing with increased short-term harvests in the East or longer term reduced harvests in the West is fundamental and has influenced economic-impact analysis in several ways, discussed in detail below.

A final important difference in economic-impact analyses is the predominance of public land in the West and private land in the East. As discussed below, private-land management can be evaluated according to price relations in wood-products markets. The Eastern component has relied on those relations in their suggestions for conducting economic-impact evaluations.

In the West, public-land managers are not necessarily motivated by the market, nor are they required to manage strictly in terms of timber markets. The Western component has therefore conducted economic-evaluation research in terms of a broader set of management objectives.

Clearly, a common and specific method of economic analysis will not be generally applicable to budworm problems. Management objectives and regional characteristics of the effects of an outbreak must be carefully considered before an evaluation is developed.

Evaluating and Responding to Budworm Outbreaks: Merchantable Yield Effects

CANUSA-East Research

Two types of budworm harvest-volume impacts are addressed in this section: tree mortality and growth losses during and after an outbreak. In the eastern half of North America, mortality losses are most important from a management perspective. Those losses are amenable to a direct evaluation. In general, those evaluations rely on the concept of net harvestable volume lost to budworm excluding any salvageable timber. Many examples of those types of evaluations are available. The Cooperative Spruce Budworm Integrated Pest-Management Program in Maine has prepared such analyses over many years.[3,4,5]

The Eastern component of CANUSA has developed more sophisticated methodology for dealing with mortality and salvage problems than simply assessing volume losses net of salvage, although that basic notion remains. Evaluating longer term silvicultural management outcomes that could offset mortality from outbreaks in the future has also been considered by economists in the East. According to Irland and Runyon (1984), however, a lack of relevant pest-management experience and data precluded any rigorous development of evaluation methodologies applicable to longer term management objectives.

In the East, economic impacts have been classified according to whether individual stands or larger forest areas were considered. Stand by stand, budworm-impacted growth and yield curves have been evaluated by Irland and Runyon (1984). They present typical histories of stand-growth loss in their paper. These authors point out that growth losses may be overstated by the typical case. Because few, if any, stands are unaffected during an outbreak, hypothetical yield curves may not be appropriate; any growth losses calculated against hypothetical yields will be overestimates. Not only may hypothetical growth losses be illusory, but live trees remaining in stands may recover

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[3] U.S. Department of Agriculture, Forest Service. 1981 spruce budworm environmental assessment. Unpublished paper on file at: Proposed Cooperative Spruce Budworm Integrated Pest Management Program, Bangor, ME.

[4] U.S. Department of Agriculture, Forest Service. 1982 spruce budworm environmental assessment. Unpublished paper on file at: Proposed Cooperative Spruce Budworm Integrated Pest Management Program, Bangor, ME.

[5] U.S. Department of Agriculture, Forest Service. 1983 spruce budworm environmental assessment. 46 p. Unpublished paper on file at: Proposed Cooperative Spruce Budworm Integrated Pest Management Program, Bangor, ME.

quickly, returning the residual stand to normal yield curves. Note, however, that little information is available on the actual response patterns of residual stands after an outbreak (Nyrop et al. 1982). Nonetheless, a consensus seems to be that mortality remains as the principal factor leading to economic losses in stands during an outbreak.

On larger acreages in the East, economic impacts of budworm are related to their influences on a manager's ability to meet three objectives (Irland and Runyon 1984):

- Maintain steady flow of host-type timber;
- Maintain high levels of tree size and quality; and
- Regulate stand distributions of species over time to maximize long-term productivity.

Heavy mortality losses during and after an outbreak will affect those objectives according to several factors. Most important seem to be the mix of host stands in a forest, duration and intensity of outbreaks, and current and future harvest patterns.

The ability of managers to cope with budworm, irrespective of projected volume losses, depends principally on the facilities available to process increased salvage, and silvicultural harvesting strategies. This issue raises some interesting problems and considerations. The point of departure for economic analysis in the East is that an outbreak is in progress. Then, if insufficient processing capacity is available to use salvage or accelerated harvest of host species, economic losses may not occur. In effect, if the timber cannot be sold, it has no value.

This notion leads to the following conclusion by Irland and Runyon (1984): Small woodlot owners may be able to salvage or accelerate the harvest, but larger landowners may not. The reasoning is that smaller harvests do not overburden processing capacity but larger harvests may not be acceptable. If the resolution of harvest value during an outbreak does indeed turn on available processing capacity, the manager who gets to market first will probably minimize economic losses.

Further, the timber-volume losses have no value in this context, primarily because harvest timing is nonoptimal. The assumption that outbreaks are in progress before economic-impact evaluations are made leads to the possibility that lost trees — or trees harvested early — have no value. Assuming management decisions can be made before an outbreak, a value should be able to be placed on the flexibility of harvest timing offered by current management options that reduce future outbreak probability. Intuitively, if a manager's trees do not die or if managers are not forced to accelerate the harvest because of an outbreak, then trees may be harvested at another date when processing capacity is available and trees may have value — a direct benefit of longer term budworm-management planning. As noted earlier, data limitations prevented such an analysis from being conducted in the East.

Even when heavy mortality is likely, several economic options in addition to salvage are open to managers. Although developed primarily for outbreak conditions in the East, much of the methodology available for dealing with expected mortality problems is applicable to outbreaks in the West as well. Irland and Runyon (1984) present a comprehensive discussion of management options and forest outcomes under a variety of Eastern outbreak damage scenarios. Nyrop et al. (1982) also discuss options available for offsetting budworm losses in the East before salvage. Marty (1984) has prepared a handbook that can be used by managers to develop precise estimates of budworm-damage effects and the net benefits of alternative management options.

CANUSA-West Research

In the West, budworm outbreaks affect different tree species than in the East. Perhaps as a consequence of longer rotations and different end uses of wood fiber, growth and yield effects have become more important. The important budworm effects on forests in the West seem to be limited to direct reductions of harvest volume in the future, acreage class rearrangements of stands, or delayed timing of planned harvest schedules. All of these effects lead to harvest-scheduling impacts. Economic research in the West has therefore focused more closely on management options that could be developed to offset budworm effects through harvest-scheduling alternatives.

In simple terms, stand and forestwide harvest scheduling is based on a set of empirical or managed yield tables developed without explicit introduction of insect- or disease-outbreak patterns. Note, however, that empirical yield tables will, by assumption, carry implicit growth impacts of historical insect and disease problems. The effect of budworm on management plans is to change the yield tables that are used to develop harvest plans, which necessitates either a control program that presumably will return forests to the original assumed yields, or responsive management that develops alternate harvest plans in response to the new, budworm-affected yield tables.

The differences in forestwide impacts between the East and West lead to another important distinction between research objectives in the two programs. Interest in the East has been on identifying several possible management responses to budworm and evaluating those responses. In the West, methodologies have been developed that would incorporate new yield tables into new optimal management plans for stands or forests. That is, management responses other than treatment are investigated in terms of the forest conditions left by the outbreak.

The difference in approach is significant, although perhaps not readily apparent. As noted earlier, outbreaks in the East are assumed to be in progress before economic evaluations are made. Heavy mortality is likely to occur in forest stands: eastern budworm impacts are expected to occur in the immediate or near future. The problem in the East is to assess management strategies that deal with the problem when it occurs. The only future planning is contained in present actions that reduce the hazard that outbreaks will reoccur.

In the West, even if an outbreak is in progress, the economic effects may not be apparent for decades.[6] When economic impacts are assessed, sufficient time may be available to develop other — perhaps better — management plans incorporating the new, budworm-affected yield tables. That is, a new plan might be developed with a value equal to or greater than the value of the old plan excluding treatment costs. Budworm could then be viewed as a net benefit. In any event, budworm stand damage might be at least partially offset by management action. Hence, even when treatment may be economically justified in terms of pre- and postoutbreak yield effects, justification may disappear when treatment is considered against a new, budworm-affected management plan. The new management plan based on budworm-affected yields could provide higher returns to forest management.

Another important distinction in the West is that outbreaks and forest impacts can be forecast with simulation models (Sheehan et al., in press). Managed responses can then be developed before an outbreak is in progress. For example, new silvicultural options, harvest schedules, or forest plans can be created to minimize expected budworm losses. These strategies can then be implemented at little or no cost relative to existing management plans.

Economic analysis and options to develop new, budworm-sensitive plans in the West have been constructed along single stand-management objectives as well as mutliple-stand, or forestwide objectives. One approach in the West has been to use dynamic programming and simulation methods to develop optimal management regimes for afffected stands. The concern was that usual analysis evaluated budworm losses against an existing or fixed set of thinning and harvesting regimes. That is, yield losses attributable to budworm were projected forward until the date of commercial thinning, or harvest that had been determined preoutbreak. Losses were then valued at that date and that value discounted to present value and compared to treatment costs. If losses were greater than treatment costs, treatment was justified. Obviously, this approach does not allow managers to respond to the new yield tables with offsetting stand-management policies.

Bible et al. (1981) demonstrated that responsive stand-thinning and harvest plans, formulated in response to expected budworm effects on yields, could offset stand losses even when no treatment was applied.

The model incorporated in that research was originally calibrated for stand-damage conditions in British Columbia. In 1983, the model was introduced in U.S. Federal Court to demonstrate the feasibility of silvicultural options that had been proposed for budworm on the Boise and Payette National Forests (*Boise Cascade* v. *Jack Lavin et al.*).[7,8] In effect, the evaluation and management stance taken was to develop a forest plan including the budworm impacts rather than simply to accept and assess those impacts in terms of existing nonoutbreak management plans.

To assess management options forestwide, two areas of investigation were followed. One problem addressed was to develop a methodology for accelerated tree removal over broad geographic areas. This problem can occur on large salvage sales or — more important in the West — when silvicultural solutions require accelerated or modified harvest timing over broad areas. Optimal control techniques were used by Bible (1982) to develop a harvest site-sequencing rule that minimized overall stand-removal costs.

Another forestwide problem addressed was to develop simple, inexpensive models for managers to use when evaluating budworm problems in terms of forestwide objectives. Budworm effects on single stands in the West can be offset by rescheduling harvests across all stands in a forest. As a consequence, budworm effects on stands should be evaluated in terms of how those effects influence forestwide objectives — after compensating changes have been made to forestwide plans.

In the West, most forest land is managed with FORPLAN,[9] or other linear-programming algorithms such as in Timber-RAM (Navon 1971; also see Johnson and Scheurman 1977). The economic impact of budworm on an entire forest would then be the difference between forestwide plan values calculated by first solving FORPLAN or Timber-RAM with normal, then with budworm-affected yields. That difference would reflect the loss attributable to budworm after compensatory changes have been made in possibly nonaffected stands.

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[6] U.S. Department of Agriculture, Forest Service. 1983 January. Environmental assessment for western spruce budworm management in eastern Oregon. 153 p. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR.

[7] U.S. Department of Agriculture, Forest Service. 1978 March. Western spruce budworm amended final environmental impact statement. 217 p. Unpublished oaper on file at: U.S. Department of Agriculture, Forest Service, Boise and Payette National Forests, State and Private Cooperation, Boise, ID.

[8] U.S. Department of Agriculture, Forest Service. 1979 April. Western spruce budworm final environmental impact statement. 39 p. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Boise and Payette National Forests, State and Private Cooperation, Boise, ID.

[9] Johnson, K. Norman; Jones, Daniel B.; Kent, Brian M. 1980 May 1. Forest Planning Model (FORPLAN), users guide and operations manual. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Systems Application Unit for Land Management Planning, Fort Collins, CO.

The main reason this approach has not been generally used is its expense. The large, linear-programming problems are confined to a single computing facility at Fort Collins, Colorado. In addition, the variable costs of developing comparative plans for the same forest but with different yield tables are unknown; often, the costs would be high. In fact, evidence indicates that budworm outbreaks may make forest-planning solutions impossible to obtain without significant redefinition of management objectives and constraints, a potentially expensive exercise.

To date, the only attempt at this type of complete analysis has been done by Bousfield et al. (1983). They used FORPLAN and PROGNOSIS-DFTM (Johnson and Scheurman 1977; Monserud and Crookston 1982; Wykoff et al. 1982) to develop full management plans with and without Douglas-fir tussock moth outbreaks. Although the need for full evaluation of insect problems forestwide has been well known for some time, conducting such an evaluation is tedious and expensive.

Part of the CANUSA research in the West addressed the problem of effort and expense in recalculating forest plans under alternate yield assumptions. The basic FORPLAN algorithm was redefined and decomposed by Berck and Bible (1984; see footnote 2). With the simpler algorithm that has resulted, forest managers should be able to calculate forestwide harvest schedules under alternate-yield assumptions much more simply and with a smaller computer. In fact, the algorithm can be run on virtually any computer system, including personal computers. The new algorithm enables managers to evaluate budworm impacts on forestwide harvest scheduling quickly and inexpensively. The program is available from either of the authors.

The basic outcome of CANUSA-West economic research on budworm effects on harvest yield has been the development of management tools. Those tools can be used to project harvest volumes and other forest outcomes over time after a budworm-management strategy has been selected. At this point, the projected harvest volumes resulting from alternative strategies can be used to evaluate treatment benefits directly. Or they can be used as inputs to the next stage of economic analysis for budworm: local and regional economic impacts.

Evaluating and Responding to Budworm Outbreaks: Local and Regional Effects

An Overview of Local and Regional Economic Effects of Budworm Outbreaks

Wood-product processing plants are placed in geographic regions where stumpage is available. Those largely private enterprises establish production capacity on several criteria of which the most important to budworm evaluation is the available wood resource in a region. Producers hold some notion of the upper and lower bounds of potential harvest volumes over time. They provide processing capacity that will take advantage of those expected harvest flows. According to Williston (1976), the principal concern of any manager evaluating the building of a processing plant is the availability of sufficient harvest volumes to operate it at — or near — full capacity. Although this notion ignores the influence of lumber markets on the ultimate profitability of a mill, it is a general rule used by producers considering either installing or abandoning plant sites.

Those producers in turn provide employment for workers who harvest, process, and distribute stumpage and other wood products. The industry also provides general-fund receipts to localities and tertiary economic benefits through industry payroll effects.

Budworm outbreaks in both the East and West can create unexpected changes in the flow of harvested timber volumes. Producer responses to such unexpected changes should be a concern of land managers. If the flow of timber is perceived as being generally uncertain in a region, the additional risk implied for producers may make capital acquisition difficult. Specifically, new mills may not be built, and existing mills may close.

Decisions not to locate a mill within a region or to close a mill already operating — with the subsequent loss of employment and local income — have potentially serious consequences for land managers. The source of future demand for harvest can be lost, and localities will suffer economically. Even without the risk that stumpage markets will not remain viable, economic losses through employment and payroll effects have the potential to be politically explosive issues for land managers.

This section of the paper discusses possible local and regional economic impacts of budworm. Research results that identify likely economic effects are reviewed. Models and data-collection procedures that will evaluate local and regional impacts are also surveyed.

CANUSA-East Research

The principal harvest effect of budworm in the East that has been suggested is an increase in present and near-term harvest volumes. Research in the East has considered the effect of those changes on harvesting and processing capacity. The focus has been on developing opportunity-loss estimates for landowners. Specifically, when processing capacity is fully used, additional harvest has no value and could reasonably be excluded from treatment. The possibility of preserving stands for later harvest when capacity is available should not be ignored, however.

Other potentially important issues have been considered in the East,but not formally addressed with an economic analysis. For example, certain silvicultural options available for budworm-susceptible stands can change the species mix in the future. Irland and Runyon (1984) and Nyrop et al. (1982) raise questions about the processing industry's ability to adapt to different species.

Minimally, forest managers need to provide timely information to wood-processing managers about possible changes in species composition. For vertically integrated firms, information will usually be passed on immediately and as a matter of course. Problems could appear, however, if many smaller landowners adopt the same silvicultural prescriptions during an outbreak.

Suppose, for example, that all small landowners adopted a CANUSA-recommended silvicultural practice that alters long-term species composition in their stands. The practice may be economically viable for each landowner considered apart, because the individual effect of the different species harvested on wood processors would likely be small. But when the aggregate effect is considered across all landowners, industry chaos could result. The effect would be a change in harvest species mix for the total harvest, not just a small part. This example is extreme, but it does highlight a consideration of potential importance in the East — especially because land tenure there is characterized by many independent land managers responsible for small areas relative to the total area affected by budworm. A potential offset for the effect could be changed technology in a region to use a different species mix. Such conjecture is beyond the scope of current management practices.

Another issue raised in the East is the potential for reduced harvest in the future resulting from accelerated harvest in the present. The problem would be exacerbated by current mortality losses. The basic issue seems to be the possibility for pulse harvesting. That could lead to a boom-bust cycle in the wood-processing sector — a high risk to capital attraction for the industry.

The potential for such problems may be great. If the reason land managers do not treat affected acreages is that without processing facilities the trees are valueless at present, then the land would be abandoned or regenerated. In an extremely large outbreak, large areas could be placed on the same rotation, leading to pulse harvesting. The problem has not been formally addressed in the East, but the phenomenon and economic consequences of pulse harvesting are discussed by Clark (1976). The basic issue for budworm management is whether maintaining a stable flow of harvest over time is possible. Resolution of that issue will require coordination of biological and economic requirements between land managers and wood processors.

CANUSA-West Research

Interest in the West has focused on the local and regional effects of harvest volume, species mix, and price changes over time in budworm habitat zones. Probable industry responses to those changes have been evaluated according to the principles of profit maximization, producer risk, and associated employment and output decisions made by producers.

The major obstacle to evaluating local and regional economic impacts of budworm has been the lack of appropriate data in both the East and West. In the West, secondary data sources were identified that would resolve the problem. Bible has developed an economic data aggregation and simulation model that provides a usable data set for regional or county economic-analysis problems.[10] Managers can use the data set produced by the model, termed CODATA, to conduct either simple or sophisticated economic analyses of probable effects resulting from changes in harvest volume and prices attributable to budworm outbreaks.

As discussed previously, the likely effect of budworm will be a reduction of harvest volumes at some point in the future. The model CODATA accepts changes in harvest volumes, species mix, and prices projected from harvest-scheduling algorithms, such as FORPLAN and Timber-RAM, as input. Those changes will reflect budworm effects through yield-table changes, but will also account for land managers' opportunities to offset budworm effects through harvest rescheduling and other management actions.

Harvest data are combined in the model with data on countywide employment in the wood-product industry, wage rates, capital costs, and other related information to obtain expected changes in industry costs and profits. The model has been calibrated and tested for the 11-year period between 1970 and 1980 and over a six-county area to evaluate possible industry responses to budworm in the West. The results of those tests are reported by Bible (1982; see footnotes 1, 10).[11,12]

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[10] Bible, T.D. 1983. CODATA: a county level simulation and data aggregation model for the Pacific Northwest wood products industry. Unpublished working paper on file at: Oregon State University, Department of Economics, Corvallis, OR.

Several interesting and provocative indications emerged from the studies. One focus of the research was to evaluate an often-voiced industry concern in response to budworm outbreaks. Industry often suggests that if harvest yield or quality falls, mills will be forced to close. That position generates political pressure for budworm treatment from localities that would be affected by mill closure. Localities then want outbreaks to be suppressed, under the assumption that budworm suppression will return forest harvests to previously projected levels, timings, and prices.

The real issues, however, are usually more complex. One issue is whether budworm treatment or nontreatment alone could cause producer profits to fall to the point where mill closure could be likely. Another is whether reduced harvests necessarily imply reduced employment. Yet another issue is the effect, if any, of budworm management on long-term economic vitality of local industry. Land managers should be able to evaluate these politically sensitive economic issues in terms of possible budworm-management outcomes.

Research in the West indicates that harvest declines can lead to increased, not decreased labor employment. Bible (see footnotes 1, 10) demonstrates that, given a fixed-processing capacity, producers appear to economize on logs when they are in short supply. That requires additional use of labor to monitor and adjust milling processes more closely. When logs are more plentiful, maximum possible output depends more on mill capacity — a function of technology and mill size — than on the number of workers. As recognized in the East, timber in excess of what can be processed with existing capacity has low value to producers. In the West, producers apparently can afford to process wood less precisely and tolerate lower recovery when it is abundant. As a consequence, less labor is needed per unit of production in the short term when wood is plentiful; more labor is needed when wood is in shorter supply. One policy implication is that mild effects of the budworm on the harvest provide positive benefits for localities in terms of employment opportunities.

In the future, newer, more technologically advanced mills may remove these labor substitution effects from producer consideration. Technological advance in the industry, however, implies that less labor will be used in wood processing relative to other inputs (see Greber and White 1982). In the future, capital inputs might exhibit the same timber substitution effects that appear for labor inputs today.

Another issue for managers to consider is whether budworm management will maintain local economic vitality. The alternative view is that certain segments of the industry in a budworm-habitat region will eventually fail with or without budworm management. Then the issue is whether budworm management is able to provide long-run stability for local economies, or simply forestalls the inevitable — budworm management may then be providing only short-term economic surpluses for producers while doing little for long-term regional economic stability.

Forestalling inevitable plant closure may describe conditions in some localities in the West (see footnote 11). The economic-data model CODATA was used to explore average profitability of the regional wood-product industry. Then the likely effects of budworm-management strategies on harvest volume and price were introduced to assess changes in regional vitality through industry profits. In at least one region, the industry appeared to be so weak that budworm strategy simply reduced losses to mill owners alone without providing any other regional economic benefits.

Note that all forest-management decisions that would affect harvest volumes, species mixes, or prices should be analyzed in terms of the broad criteria outlined here. Decisions made for forests may influence decisions made further on in wood-product processing. Those issues can be politically sensitive. Managers must consider and, when possible, evaluate the validity of local and regional claims for expected damages.

Evaluating and Responding to Budworm Outbreaks: Recreation and Scenic Effects

Budworm defoliation may have an impact on recreational use. The transmission mechanism for those effects is straightforward. Defoliators can visually blight an area. People may not be happy pursuing recreation in visually blighted areas. Hence, areas that depend on recreation may suffer income losses when recreation visits decrease.

Although recognized, these issues have not been actively pursued by CANUSA for several reasons. Earlier research into recreation losses caused by defoliators has been inconclusive. In the Northeast, researchers were unable to demonstrate changes in

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[11] Bible, T.D. 1983. Economic concepts and methods for evaluating insect and disease problems on forest lands. Unpublished working paper on file at: Oregon State University, Department of Economics, Corvallis, OR.

[12] Bible, T.D. 1983. Returns to capital in lumber manufacturing: actual and opportunity costs for an Oregon County. Unpublished working paper on file at: Oregon State University, Department of Economics, Corvallis, OR.

recreation-use patterns that could be attributed to gypsy moth defoliation (White and Schneeberger 1981). In the Northwest, similar results were obtained for Douglas-fir tussock moth defoliation (Downing et al. 1977). The obvious implication is that budworm defoliation and mortality would not significantly affect recreation-use patterns when other defoliators have had no impact.

Attention in the Northeast and Northwest has therefore focused on budworm impacts on merchantable timber yields. Yield and merchantability problems are the dominant budworm effects in those regions and receive the most public attention. Economic research has been more effectively applied to harvest problems in those areas because those problems are most significant there.

In the southwestern United States and the front range of the U.S. Rocky Mountains, the situation is somewhat different. Harvest yields are already low compared to Northeast and Northwest harvests, tree size and quality is not high, and — as a consequence — timber management is not the principal forest-management concern. A focus of budworm-impact research in those regions has been on other, regionally important issues — including recreation and water quality.

Research into scenic and recreational impacts of budworm has also been influenced by methodological advances by Buyhoff et al. (1982). Earlier studies of the recreation effects of defoliators have been hampered by the lack of reliable theoretical and methodological foundations for evaluating those effects. Daniel and Buyhoff, working together and independently, have resolved many of those issues.

Of particular interest in this connection is research funded by the U.S. Forest Service through Region 2's Forest Pest Management, Cooperative Forestry Branch. Daniel, Buyhoff, Schroeder, and Walsh have developed, in collaboration and independently, quantitative measures of visual impairment and are linking those to recreational expenditure patterns (Buyhoff et al. 1982; Schroeder and Daniel 1981).[13,14,15]

The basic, but as yet unresolved, issue is whether tree defoliation and mortality lead to losses in recreational value for individuals and regions that would justify budworm treatment. This issue is certain to gain more attention in the future. Managers are expressing more interest in these concerns, especially in the Southwest. For example, the issue has been included — but not quantitatively addressed — in at least two environmental assessments prepared for budworm problems in New Mexico and Arizona.[16,17]

Land-Tenure Influences on Budworm-Management Strategy

Land-tenure considerations enter budworm economic-impact assessment through specific land-management objectives for affected sites. In effect, different tenure assumptions can place different relative values on the same, or similar, biological and forest situations. Different management decisions may be the result. An example can make this point clear. Assume that a budworm outbreak is in progress or impending. The outbreak is likely to lead to losses in harvest volume. Then, private, independent landowners will make budworm-management decisions to maximize dollar returns to their own holdings. Decisions will be made in terms of the direct costs and benefits accruing to stand management by owners. Using methodology similar to that outlined by Marty (1984), a decision that maximizes net present value of stand management would be made. Others that could be affected by budworm management could be ignored by land managers unless obvious interactions between welfare of those others and the land manager are evident. Thus a land manager would only be concerned about mill-owners' problems when changes at mills caused by budworm management would lead to additional, perhaps indirect, effects for land managers.

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[13] Daniel, T.C. 1981. Assessment of public perceptions and values regarding mountain pine beetle and western spruce budworm impact in the Colorado Front Range. 36 p. Unpublished final report on file at: U.S. Department of Agriculture, Forest Service, Forest Insect and Disease Management, Lakewood, CO.

[14] Walsh, R.G.; Keleta, G.; Olienyk, J.P. 1981. Value of trees to residential property owners with mountain pine beetle and spruce budworm damage in the Colorado Front Range. 115 p. Unpublished paper on file at: Colorado State University, Department of Economics, Fort Collins, CO.

[15] Agricultural Enterprises, Inc. 1981. Impact assessment of mountain pine beetle and western spruce budworm. 218 p. Unpublished final report on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Lakewood, CO.

[16] U.S. Department of Agriculture, Forest Service. 1983. Draft environmental impact statement, western spruce budworm management program, Santa Fe National Forest. 121 p. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Southwestern Region, Albuquerque, NM.

[17] U.S. Department of Agriculture, Forest Service. 1981. Environmental impact statement, western spruce budworm management plan, Carson National Forest. 43 p. Unpublished paper on file at: U.S. Department of Agriculture, Forest Service, Southwestern Region, Albuquerque, NM.

In the United States public sector, different approaches might be taken. Public-land managers are required by law to consider the effect on local producers and regional economies when budworm-management actions are taken. In fact, when the issue involves a choice between maximizing timber-receipts on public lands and local economic vitality or stability, timber-receipt objectives may be abandoned. Exceptions in the West occur on some state lands where net timber receipts must be maximized under statutory regulations.

In a third tenure situation, tree farm licenses in Canada generally provide that private managers control operations on Crown lands. Those who do not use efficient practices on Crown lands may lose their timber rights on those lands. Then, private managers on public lands may develop entirely different budworm-management strategies than in either of the examples considered above.

Thus, the same budworm problem could result in at least three different management approaches. The underlying difference could be the land tenure of the forest that influences management objectives.

This is the key principle underlying the issues raised by Bible (see footnote 1), Irland and Runyon (1984), and Nyrop et al. (1982): The objectives of the manager are the single most important criterion when budworm effects are evaluated. No universal management responses to budworm exist, only a methodology for developing and evaluating those responses in terms of management objectives.

These issues and concerns are not new. What is new is the much wider range of management objectives and options than has been available in the past. Direct suppression once seemed to be a universal panacea for problems with forest defoliation. Previous management approaches were valid in three contexts: in terms of early, more narrow land-management objectives that sought to maximize or sustain the flow of harvested timber over time; in terms of the limited silvicultural and responsive management experience in dealing with insect and disease problems; and finally, in terms of the homogeneous political constituency that believed themselves to be affected by land-management decisions.

Today, and in the future, forest managers face a wide variety of interrelated objectives. In addition, a wide range of responsive management practices have been and are being developed. And last — but not least important to managers — the political constituency that must be considered when forest policy is developed has become broad and heterogeneous. Conflicting and often incompatible goals have been mandated to managers, and those will complicate any analysis. Because of these and related factors, choosing an optimal budworm strategy will critically depend on management's ability to define their objectives clearly in terms of alternative policies, affected constituencies, and land-tenure requirements.

Literature Cited

Berck, P.; Bible, T.D. 1984. Solving and interpreting large scale harvest scheduling problems by duality and decomposition. For. Sci. 30(1):173-182.

Bible, T.D. 1982. Harvesting site sequencing and optimal stopping rules for harvesting multiple sale blocks over time. For. Sci. 28(4):697-705.

Bible, T.D.; Brodie, J.D.; Kao, C. 1981. Optimal harvest and thinning regimes for stands subject to episodic insect damage. Pages 145–149 *in* Land-use allocation: processes, people, politics, professionals. Proc. 1980 Conv. Soc. Am. For., Washington, D.C.

Blum, B.T.; MacLean, D.A. 1985. Potential silviculture, harvesting, and salvage practices in eastern North America. Pages 264-280 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Boise Cascade Corporation v. *Jack Lavin et al*., and Consolidated Actions. Civil Nos. 81-1357, 81-1369, 81-1433. (U.S. Dist. Court, Idaho 1983).

Bousfield, W.E.; Quinn, T.; Lewis, J. (et al.). 1983. Economics of Douglas-fir tussock moth control. U.S. Dep. Agric., For. Serv., For. Pest Manage., Washington, D.C. 58 p.

Brookes, M.H.; Campbell, R.W.; Colbert, J.J.; Mitchell, R.G.; Stark, R.W., tech. coords. (In press). a. Western spruce budworm. U.S. Dep. Agric., Washington, D.C. Tech. Bull. 1694.

Brookes, M.H.; Colbert, J.J.; Mitchell, R.G.; Stark, R.W., tech. coords. (In press). b. Managing trees and stands susceptible to western spruce budworm. U.S. Dep. Agric., Washington, D.C. Tech. Bull. 1695.

Brookes, M.H.; Colbert, J.J.; Mitchell, R.G.; Stark, R.W., tech. coords. (In press). c. Western spruce budworm and forest-management planning. U.S. Dep. Agric., Washington, D.C. Tech. Bull.

Buyhoff, G.J.; Wellman, J.D.; Daniel, T.C. 1982. Predicting scenic quality for mountain pine beetle and western spruce budworm damaged forest vistas. For. Sci. 28(4):827-838.

Carlson, C.E.; Schmidt, W.C.; Fellin, D.G.; Wulf, N.W. 1985. Silvicultural approaches to western spruce budworm management in the northern U.S. Rocky Mountains. Pages 281-300 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworm research. Proc. CANUSA Spruce Budworms Research Symp. 16-20, Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Clark, Colin W. Mathematical bioeconomics. 1976. John Wiley and Sons, New York. 352 p.

Downing, K.B.; Debucchi, P.B.; Williams, W.R. 1977. Impact of the Douglas-fir tussock moth on forest recreation in the Blue Mountains. U.S. Dep. Agric., For. Serv., Portland, Oreg. Res. Pap. PNW-224. 14 p.

Greber, B.J.; White, D.E. 1982. Technical change and productivity growth in the lumber and wood products industry. For. Sci. 28(1):135-147.

Irland, L.C.; Runyon, K.L. 1984. Economics of spruce budworm management strategy, Chapter 5 *in* Proc. CANUSA-East Symp. U.S. Dep. Agric., For. Serv., Washington, D.C.

Johnson, K.N.; Scheurman, H.L. 1977. Techniques for prescribing optimal timber harvest and investment under different objectives: discussion and synthesis. For. Sci. Monogr. 18. 31 p.

Marty, R. 1984. A guide to economic evaluation of spruce budworm management opportunities. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 627.

Monserud, R.A.; Crookston, N. 1982. A user's guide to the combined stand prognosis and Douglas-fir tussock moth outbreak model. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, Utah. Gen. Tech. Rep. INT-140. 65 p.

Navon, D.I. 1971. Timber RAM: a long range planning method for commercial timber lands under multiple use management. U.S. Dep. Agric., For. Serv., Pac. Southwest For. and Range Exp. Stn., Berkeley, Calif. Res. Pap. PSW-70. 22 p.

Nyrop, J.P.; Simmons, G.A.; Mosher, D.G. 1982. The economics of pre-salvage alternatives as a method of minimizing spruce budworm losses. Mich. Coop. For. Pest Manage. Program, Mich. Agric. Exp. Stn, East Lansing, Mich. Tech. Rep. 82-9. 57 p.

Schroeder, H.; Daniel, T.C. 1981. Progress in predicting the perceived scenic beauty of forest landscapes. For. Sci. 27(1):71-80.

Sheehan, K.; Crookston, N.L.; Kemp, W.P.; Colbert, J.J. (In Press). Modeling budworm and its hosts. Chapter 8 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech. coords. Western spruce budworm, U.S. Dep. Agric., Washington, D.C. Tech. Bull.

White, W.B.; Schneeberger, N.F. 1981. Socioeconomic impacts. Pages 681-694 *in* The gypsy moth: research towards integrated pest management. U.S. Dep. Agric., For. Serv., Gypsy Moth Res. and Dev. Program, Washington, D.C.

Williston, E.M. 1976. Lumber manufacturing. Miller Freeman Publications, Inc., San Francisco, Calif. 512 p.

Wykoff, W.R.; Crookston, N.L.; Stage, A.R. 1982. User's guide to the stand prognosis model. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, Utah. 102 p.

Forest Fire Behavior in Spruce Budworm-Killed Balsam Fir

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An intensive experimental burning program was carried out in Ontario between 1978 and 1982, in order to quantitatively document fire behavior in balsam fir mortality resulting from an eastern spruce budworm infestation. Forest fire potential in budworm-killed balsam fir was shown to be significantly increased for a number of years following stand mortality. Crown breakage and wind throw, with resultant fuel complex rearrangement and increased surface fuel loadings, peaks 5-8 years after mortality. Fire potential is greatest during this period, decreasing gradually as balsam fir surface fuel begins to decompose and understory vegetation proliferates. Spring fires, occurring prior to flushing, behave explosively with continuous crowning, high spread rates, and severe downwind spot fire problems. Summer fires in this fuel type do not spread at all in the early years following mortality; however, sufficient surface fuel accumulation 4-5 years after mortality will permit summer fire spread. Western studies were limited; no significant short- or long-term effects on fire potential or intensity were noted, primarily because there is little mortality of host species as a result of defoliation.

Entre 1978 et 1982, une campagne intensive de brûlages expérimentaux a été réalisée en Ontario, afin de mesurer le comportement du feu dans le peuplements de sapin baumier tués par la tordeuse des bourgeons de l'épinette. Le risque d'incendie dans ces sapinières s'est révélé notablement accru, pendant un certain nombre d'années subséquentes à la mortalité. Le bris des houppiers et le déracinement des arbres par le vent modifient le complexe de combustibles et en accroissent l'apport au sol, de sorte que le risque culmine cinq à huit ans après la mortalité, après quoi il diminue graduellement à mesure que le combustible de surface fourni par les sapins commence à se décomposer et que la végétation du couvert prolifère. Les incendies printaniers, qui se déclarent avant le débourrement, ont un comportement explosif, avec feux de cimes continus, à propagation rapide, et apparition de nombreux foyers disséminés sous le vent. Ceux d'été ne se propagent pas du tout au cours des premières années consécutives à la mortalité; toutefois, quatre ou cinq ans après, il s'est accumulé au sol suffisamment de combustible pour en permettre la propagation. Dans l'Ouest, les études ont été limitées; on n'a noté aucun effet notable à court ou à long terme sur le risque ou l'intensité de l'incendie, surtout à cause de la faible mortalité d'hôtes par suite de la défoliation.

Introduction

Outbreaks of forest insects that result in extensive tree mortality can drastically alter fire hazard and potential fire behavior. For many years, entomologists have referred in a qualitative sense to increased forest fire hazard resulting from forest insects (e.g., Graham 1923; Swaine et al. 1924; Prebble 1950; Baskerville 1975; Furniss and Carolin 1977). This assumption would seem reasonable in view of the large increase in the quantity of dead and dry material available for combustion following tree mortality, and the significant effect this increase in available fuel would have on fire behavior and attendant fire control problems.

Prior to the CANUSA Spruce Budworms Program, however, little quantitative evidence existed on the effects of insect outbreaks on the incidence and severity of forest fire. The intermittent and unpredictable occurrence of outbreaks, the size and complexity of adequate studies, and the time needed to obtain adequate data, generally precluded such studies. Forest fire managers, understandably, have been divided in their opinions on the forest fire potential of infested forests.

Limited studies were conducted in western forests to determine the short- and long-term effects of western spruce budworm (*Choristoneura occidentalis* Free.) outbreaks (Martin and Olson 1978[1], 1980[2]). It was concluded that ground and surface fires would be little affected by severe defoliation except for slight microclimate changes due to increased insulation. Further, although significantly greater loads of litter and downed wood 2.5 to 7.6 cm (1 to 3 in) in diameter were found in defoliated stands, potential fire rates of spread (Rothermel 1972) were not significantly increased.

Eastern and western spruce budworm outbreaks are not comparable. Western spruce budworm outbreaks are generally of relatively short duration, are less extensive in area, and tree mortality is minimal (Carlson et al. 1983). Outbreaks of the eastern spruce budworm are notably different.

Historical records indicate that past spruce budworm (*Choristoneura fumiferana* (Clem.) infestations in eastern North America have generally been succeeded, within 5-10 years, by severe forest fires. The Miramichi Fire of 1825 in New Brunswick (Flieger 1970), the Isle Royale Fire of 1936 in Minnesota (Hansen et al. 1973), and the Chapleau-Mississagi Fire of 1948 in Ontario (Stocks and Walker 1973) are prominent examples of large forest fires associated with vast areas of dead balsam fir (*Abies balsamea* (L.) Mill.) resulting from spruce budworm infestations. Until recently there had been no quantitative evaluation of the rate and magnitude of change within the balsam fir fuel complex following budworm infestations, and no quantitative assessment of the impact of these changes on subsequent forest fire behavior.

The most recent spruce budworm outbreak in eastern North America, during the 1970s, provided the opportunity to conduct a thorough investigation into balsam fir stand decomposition following mortality, associated fuel arrangement changes through tree crown breakage and surface fuel accumulation, and the overall impact of this process on forest fire potential in this fuel type. A study was initiated in Ontario in 1976, in which balsam fir fuels were inventoried for several years following mortality, and a series of well-monitored experimental fires were conducted under a broad range of fire weather conditions to document fire behavior parameters in a quantitative manner. This was a logical extension of an experimental burning program underway in major Ontario forest fuel types (Stocks 1977), as a cooperative endeavor between the Great Lakes Forest Research Centre (GLFRC) Forest Fire Research Unit and the Ontario Ministry of Natural Resources (OMNR) to develop fire behavior prediction guidelines for fire management purposes. In addition to this work in Ontario, Canadian Forestry Service (CFS) fire researchers from the Petawawa National Forestry Institute (PNFI) have been measuring surface fuel accumulation in dead balsam fir stands in the Cape Breton Highlands of Nova Scotia in recent years. No results from this study are available at this time and no experimental burning is planned in that area.

Study Area Description

In northeastern Ontario, fir grows in a heterogeneous mix with a variety of species, often as an understory component. Because of this growth pattern, it was difficult to find a research test area that was representative, but in 1976 an area on the Aubinadong River (latitude 46°53'N, longitude 83°24'W) in central Ontario (80 km NE of Sault Ste. Marie) was selected for the establishment of experimental burning plots. The study site is located in the transition zone between the Algoma and Timagami Sections of the Great Lakes-St. Lawrence Forest Region (Rowe 1972) where forests are very mixed in nature — red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), jack pine (*Pinus banksiana* Lamb.), white spruce (*Picea glauca* (Moench) Voss), and balsam fir growing in association with poplar (*Populus* spp.), maple (*Acer* spp.) and birch (*Betula* spp.). The climate in this area is characterized by short, warm summers, (mean daily July temperature 16°C [61°F], and long, cold winters (mean daily January temperature −17°C [1.4°F]), with a mean annual precipitation of 760 mm (30 in), of which a 250 mm (10 in) water equivalent falls as snow (Chapman and Thomas 1968).

The most striking characteristic of the forest at the Aubinadong River study site is the predominance of dead balsam fir. A very sparse overstory of decadent pine, spruce, and birch exists on the site, but is underlaid with a continuous substratum of dead fir (Figures 1(a) and 1(b)). The area was logged for sawlog material in the early 1960s, and fire-scar analysis indicates the last wildfire on this site occurred in approximately 1770. These two factors have combined in conjunction with the most recent spruce budworm infestation, to produce the current Aubinadong River fuel complex.

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[1] Martin, R.E. and C.M. Olson. 1978. Preliminary evaluation of short-term fire hazard modification caused by western spruce budworm outbreaks. Canada/United States Spruce Budworms Program-West. Final Report. Pacific Northwest Forest and Range Experiment Station. Portland, OR. Unpubl. 40 p.

[2] Martin, R.E. and C.M. Olson. 1980. Evaluation of long-term fire hazard resulting from western spruce budworm defoliation. Canada/United States Spruce Budworms Program-West. Final Report. Pacific Northwest Forest and Range Experiment Station. Portland, OR. Unpubl. 30 p.

The latest spruce budworm outbreak was first noticed on this site in 1972 (Howse et al. 1973) and after repeated annual infestations and defoliation, virtually 100 percent of the balsam fir were dead by 1977-1978. The large preponderance of dead balsam fir on the Aubinadong River site is illustrated in Table 1. More than 2100 dead balsam fir stems per hectare are present, accounting for 80 percent of the stems ≥3.0 cm (1 in) diameter breast height (DBH) on site. In addition to the figures shown in Table 1, an average of 850 dead balsam fir and 80 spruce stems <3.0 cm (1 in) DBH were also present. Figures 2(a) and 2(b), outlining diameter and height distributions for both the dead balsam fir and live spruce components of the Aubinadong River forest, show the overwhelming proportion of dead balsam fir to be in the smaller size classes, averaging 9.6 cm (3.7 in) in diameter breast height (DBH) and 8.2 m (27 ft) in height. The live spruce, many of which were partially defoliated by the budworm, were slightly larger. Stand composition data were compiled using a systematic sampling approach, involving the use of point centre quarter (PCQ) method plots (Cottam and Curtis 1956) for trees ≥3.0 cm (1 in) DBH, and a series of 2-m (6 ft) radius fixed plots for trees <3.0 cm (1 in) DBH.

A series of 10, 2-ha (5-acre) experimental burning plots were established at the Aubinadong River site in 1976 by GLFRC Fire Research personnel. Each plot was square (141.4 m × 141.4 m [464 ft × 464 ft]) and surrounded by a 20-m (65-ft) wide fireline, bulldozed to mineral soil (Figure 3). A complete fire weather station was established on site and daily observations at 1300 hr of temperature, relative humidity, wind velocity, and precipitation were taken to calculate the various fuel moisture codes and fire behavior indices of the Canadian Forest Fire Weather Index (FWI) System (Can. For. Serv. 1984). It was planned to conduct both spring and summer experimental fires, over a number of years and under a variety of fire weather conditions. However, the third fire conducted in the spring of 1981 escaped control and burned over the remaining plots. This necessitated the establishment of three additional burning plots, of the same dimensions, at the Aubinadong site. These plots were burned in 1982.

Figure 1(a) and (b). Dead balsam fir and spruce, decadent overstory pine and spruce — Aubinadong River.

Table 1
Average stand structure characteristics for 13 experimental burning plots at the Aubinadong River study area, based on cruise data for live and dead stems ≥ 3.0 cm DBH

Species	Stems/ha			DBH (cm)			Height (m)		
	$\bar{y}$[1]	SD[1]	$S\bar{y}$[1]	$\bar{y}$[1]	SD[1]	$S\bar{y}$[1]	$\bar{y}$[1]	SD[1]	$S\bar{y}$[1]
Balsam fir[2]	2121	1044	289	9.6	2.3	0.6	8.2	1.4	0.4
Black spruce	229	197	92	12.1	3.3	0.9	8.7	1.5	0.4
Others[3]	302	92	26	—	—	—	—	—	—

[1] Where $\bar{y}$ *represents the mean, SD the standard deviation, and* $S\bar{y}$ *the standard error of the mean.*
[2] *Dead stems.*
[3] *Jack pine, red pine, white spruce, and white birch.*

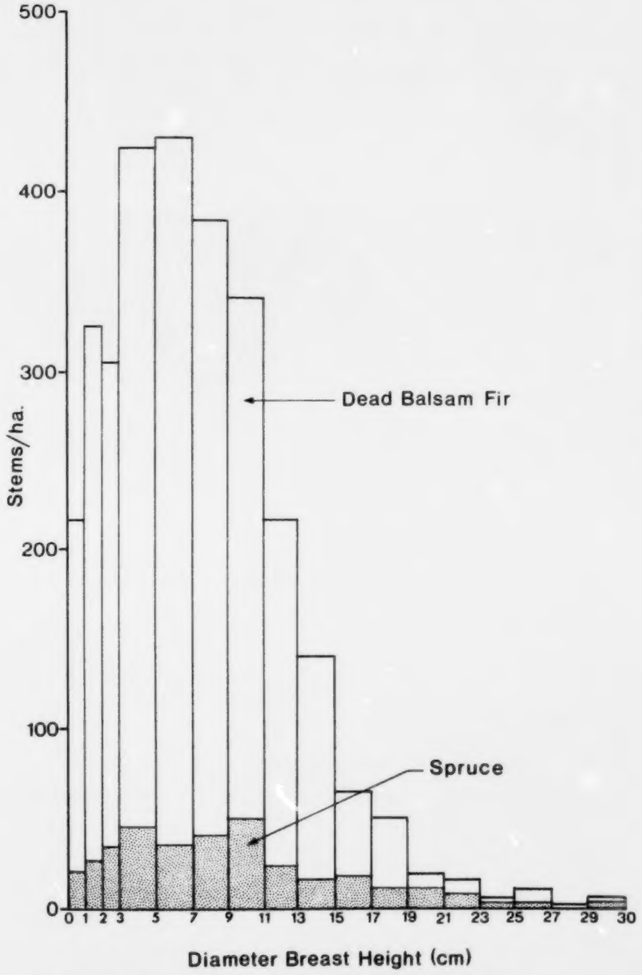

Figure 2(a). Diameter Distribution — Aubinadong River.

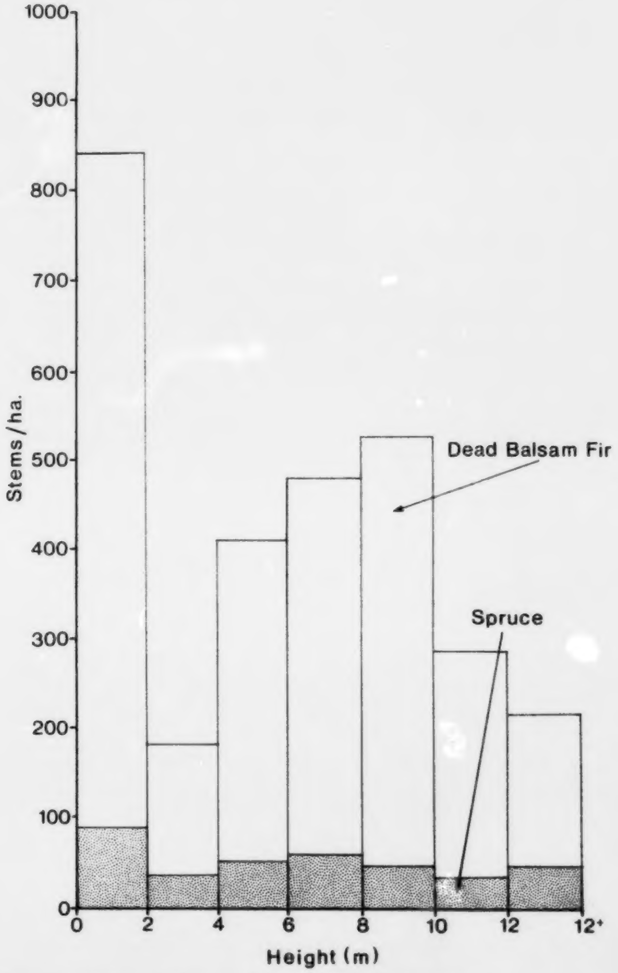

Figure 2(b). Height Distribution — Aubinadong River.

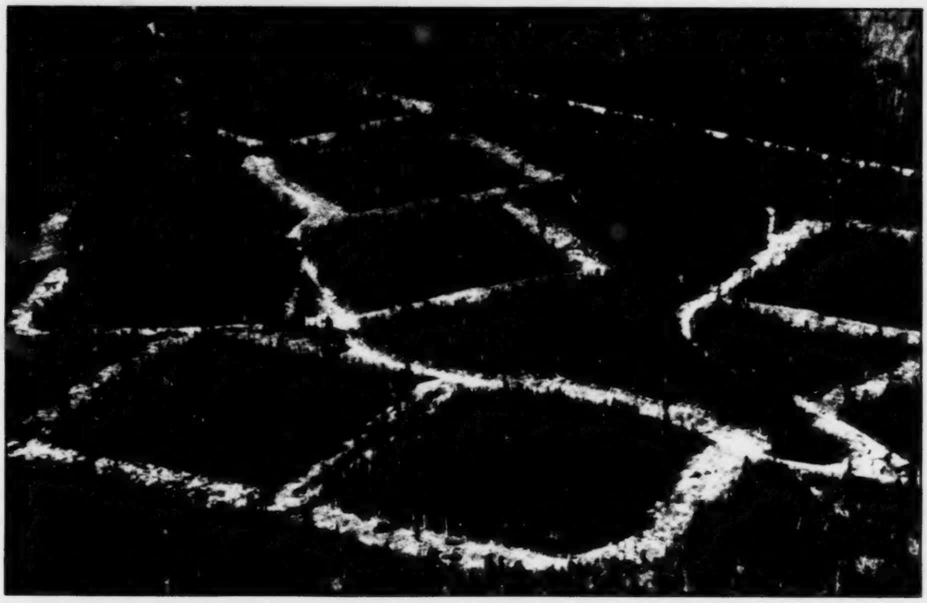

Figure 3. Arrangement of 2-ha burning plots with 20-m firelines — Aubinadong River.

The Balsam Fir Fuel Complex

A systematic grid pattern was established in each experimental burn plot (Figure 4) and a variety of sampling techniques were used to monitor in detail the quantity and distribution of all ground, surface, and aerial fuels.

(a) Ground Fuels

Ground fuels, or that organic material layer above the mineral soil, were sampled at 36 locations in each burning plot. Samples 0.5 m × 0.5 m (20 in × 20 in) were cut from the ground, sectioned horizontally into 2-cm (1 in) thick layers and grouped by plot. Bulk density figures for each layer were determined by oven-drying and adjusting for ash content. Average bulk densities for the Aubinadong River plots are presented in Table 2 and show a dense compacted organic mantle on this site. Surface litter was a reflection of the heterogeneous nature of the stand, consisting of a mixture of feather moss, conifer needles, and hardwood leaves.

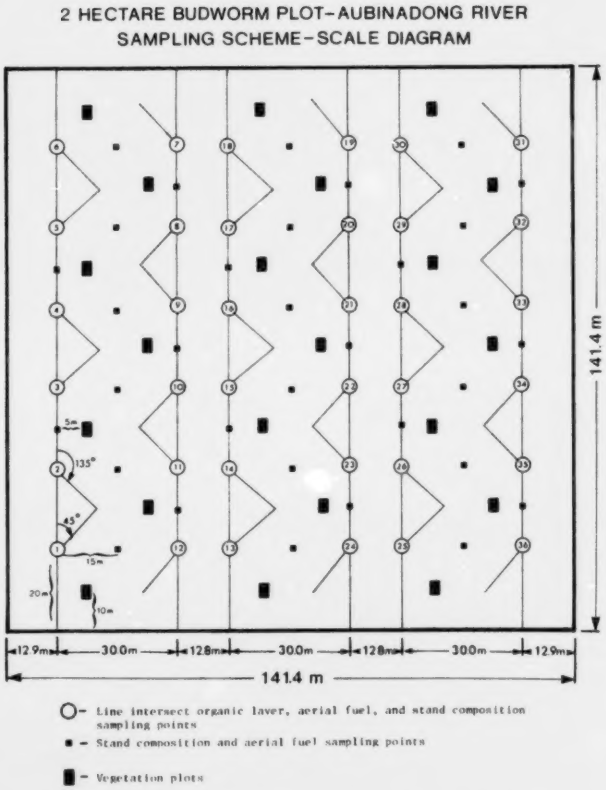
2 HECTARE BUDWORM PLOT-AUBINADONG RIVER
SAMPLING SCHEME-SCALE DIAGRAM
141.4 m
5m
135°
45°
15m
20m
10m
12.9m
30.0m
12.8m
30.0m
12.8m
30.0m
12.9m
141.4 m
○ – Line intersect organic layer, aerial fuel, and stand composition sampling points
■ – Stand composition and aerial fuel sampling points
█ – Vegetation plots

Figure 4. 2-ha budworm plot — Aubinadong River sampling scheme — scale diagram.

Table 2

Average organic layer depth and weights for 10 experimental burning plots at the Aubinadong River study area

Statistic[1]	Depth (cm)	Weight by depth class (kg/m²) 0-2 cm	2-4 cm	4-6 cm	6-8 cm	8+ cm	Total
$\bar{y}$	7.00	0.825	1.214	1.687	2.233	1.975	7.934
SD	0.66	0.092	0.180	0.286	0.562	0.718	1.535
$S\bar{y}$	0.21	0.031	0.060	0.096	0.187	0.239	0.512

[1] *Where $\bar{y}$ represents the mean, SD the standard deviation, and $S\bar{y}$ the standard error of the mean.*

(b) Surface Fuels

Both downed dead woody material and low herbaceous and shrub vegetation were considered as surface fuels in this study. Vegetation weights were determined by collecting and oven-drying biomass samples from 21 subplots (2 m × 3 m [2.5 ft × 10 ft]) in each burning plot. The line intersect sampling technique (Van Wagner 1968) was used to inventory woody surface fuels on 36 permanent 15-m (50 ft) transects located in each burning plot. Surface fuel oven-dry weight figures, based on 1977 sampling, are presented in Table 3. Large rotten logs, resulting from earlier logging operations and general stand decadence, contribute significantly to surface fuel loading totals.

Permanent woody surface fuel transects in each burning plot were remeasured each year to monitor surface fuel accumulation, through balsam fir crown breakage and windthrow, as stand decomposition accelerated during the years following mortality. Figure 5 illustrates the dramatic increase in balsam fir surface fuel accumulation during the 5 years following balsam fir mortality at the Aubinadong River site. During the same period, permanent surface fuel accumulation transects were established and monitored near Gogama, 180 km (112 mi.) northeast of the Aubinadong River, and an area in which heavy balsam fir mortality was occurring. Surface fuel accumulation figures for the Gogama transects exhibit the same trends evident at the Aubinadong River site (Figure 5).

Top breakage on all burning plots was monitored during the 1978-1982 period, and rose steadily from 6 percent in 1978 to more than 70 percent by 1982, paralleling the rise in surface fuel loadings.

Table 3

Average surface fuel weights (kg/m²) for 10 experimental burning plots at the Aubinadong River study area in 1977

Statistic[1]	Lesser vegetation Herbaceous	Shrubs	Roundwood fuels by diameter size class 0-1 cm	0-3 cm	0-7 cm	7+ cm sound	7+ cm rotten
$\bar{y}$	0.028	0.165	0.127	0.257	0.417	0.315	3.163
SD	0.015	0.061	0.039	0.065	0.096	0.582	0.590
$S\bar{y}$	0.006	0.025	0.012	0.021	0.031	0.184	0.187

[1] *Where $\bar{y}$ represents the mean, SD the standard deviation, and $S\bar{y}$ the standard error of the mean.*

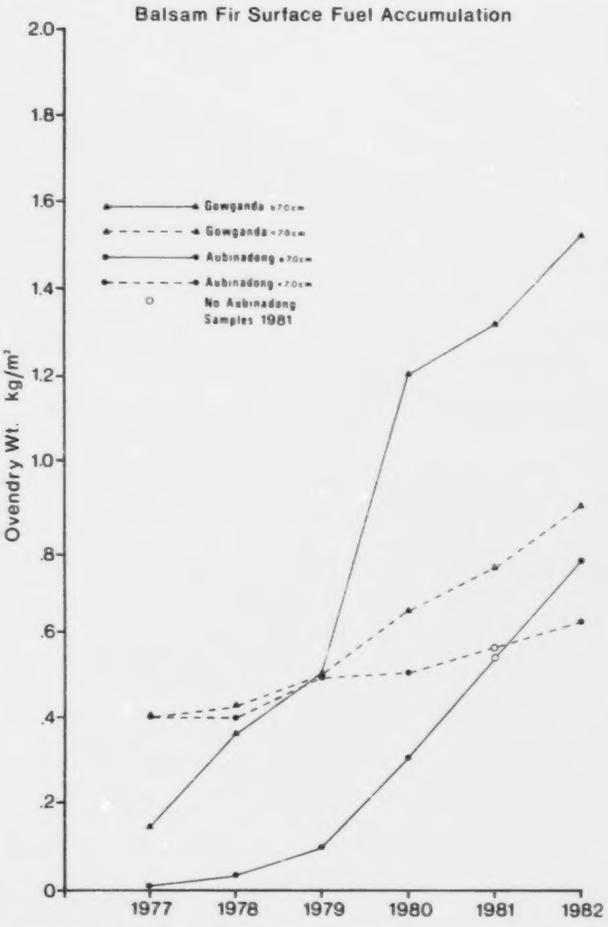

Figure 5. Balsam fir surface fuel accumulation.

Table 4
Average aerial fuel weights (kg/m²) for 13 experimental burning plots at the Aubinadong River study area

Statistic[1]	Balsam fir			Spruce		
	<1.0 cm	<3.0 cm	Total crown	Foliage	<1.0 cm	Total crown
$\bar{y}$	0.997	1.557	4.286	0.539	0.642	0.932
SD	0.283	0.387	1.187	0.403	0.415	0.693
$S\bar{y}$	0.085	0.117	0.358	0.122	0.125	0.209

[1] *Where $\bar{y}$ represents the mean, SD the standard deviation, and $S\bar{y}$ the standard error of the mean.*

(c) Aerial Fuels

Crown fuel component weights for dead balsam fir were determined by destructively sampling trees of various sizes. Crown fuels were separated into size classes, oven-dried, and weighed. Curves predicting crown component weights were developed using DBH as the independent variable (Kent 1978). Spruce crown weights were calculated using relationships developed in an earlier Ontario study (Walker and Stocks 1975).

These crown component weights were combined with stand density data gathered on each burning plot, using the PCQ and fixed-radius plot methods described earlier to determine the overall aerial fuel loadings outlined in Table 4. No estimate of deciduous aerial fuels was attempted since hardwood trees were a minor component in the Aubinadong River forest and did not contribute to overall fire behavior.

Experimental Burning

(a) Procedure

It was intended that experimental fires would be conducted over several years at the Aubinadong River site, burning only one or two plots a year, to assess the impact of surface fuel accumulation on fire behavior. It was suspected that stand breakup following mortality would result in balsam fir crown fuels being closer to the ground, and therefore more available for combustion. Stand deterioration also opens up the forest canopy, resulting in a significant increase in the amount of solar radiation reaching the forest floor and, consequently, a dramatic increase in understory vegetation growth. It was felt that this process would retard fire spread in fires occurring after the flushing of understory vegetation in early June. As a result, both spring and summer experimental fires were planned, so that results could be compared.

Ignition, control, and suppression of all experimental fires was the responsibility of OMNR fire management personnel. Several well-equipped fire crews, with helicopter and water bomber support, were used on each burn. GLFRC Fire Research Unit staff monitored and documented fire behavior parameters on each fire, through both air and ground observation.

Prior to ignition, surface and aerial fuels were remeasured and 300 depth-of-burn pins were systematically placed throughout the plot. These pins were driven into the ground so that a horizontal t-bar on each pin was flush with the top of the organic layer. Moisture content samples were collected from selected fuels on each plot and fire weather calculations were updated immediately before each experimental fire.

All experimental fires were ignited along a windward boundary and allowed to burn with the wind to achieve an equilibrium spread rate quickly, and thereby simulate a free burning wildfire as much as possible. Plots were ignited along two adjacent boundaries if the wind direction was on a plot corner rather than a side.

Forward rate-or-spread was measured using stop watches on the ground to time the arrival of the fire front at grid points and, on particularly fast-spreading fires, through filming from a helicopter. Fire behavior was documented using both slide and movie film.

Post-burn sampling was carried out within a few hours of each fire. Surface fuels were remeasured on each transect to determine post-burn loadings and therefore surface fuel consumption. Aerial fuel consumption was measured at each PCQ plot and fixed-radius plot located earlier. Depth-of-burn was measured on each t-bar pin, averaged for each plot, and converted to a fuel weight consumption using the bulk density figures calculated previously for each ground fuel layer.

(b) Results

Between 1978 and 1982, eight experimental fires were attempted at the Aubinadong River site. Six of these fires were successful while two burns were incomplete. Experimental burning began in May 1978 with two highly successful, fast-spreading fires under spring conditions. Poor burning weather during the summer of 1978 precluded further fires. Two incomplete fires were attempted in 1979 — the first while understory vegetation was partially flushed and the second a month after flushing was complete. The first 1979 fire burned 30 percent of the plot before going out, while the second 1979 fire did not spread at all. A severe wildfire situation in Ontario throughout the spring and summer of 1980 left no resources for experimental burning that year and the next Aubinadong River burn was ignited in May 1981. This fire escaped control, burning over all of the remaining plots and 40 hectares (100 acres) of surrounding forest because of a wind-shift soon after ignition. As mentioned earlier, three additional plots were established in late 1981 to replace those lost in the escaped fire. These plots were successfully burned in 1982, two before and the final plot after understory flushing. No spread data are available for one of the 1982 spring fires as this fire was the result of an unplanned ignition (suspected campfire) when no one was present to monitor behavior. However, the plot had been completely set up for burning and, therefore, fuel consumption data could be compiled. Tables 5 and 6 show complete fire behavior and fire weather data gathered on the Aubinadong River burns. Table 5 outlines fuel consumption figures for various fuel strata, whereas Table 6 gives total fuel consumption figures, along with forward rate of spread, fire intensity and fire weather data.

Frontal fire intensity figures, in kilowatts per metre (kW/m) were calculated by the equation (Byram 1959):

$$I = Hwr$$

where H is the fuel low heat of combustion, in kilojoules per kilogram (kJ/kg); w is the weight of fuel consumed (in the active flaming zone), in kilograms per square metre (kg/m^2); r is the rate of spread in metres per second (m/s). For the purpose of calculating the intensity values shown in Table 6, all organic and surface fuel (both woody material and surface vegetation) consumption measured for each fire was considered to have been consumed in the flaming front. In addition, dead balsam fir aerial fuels ≤ 1.0 cm in diameter and all live spruce foliage, were also assumed to have been consumed in the active flaming zone. Any consumption of rotten logs or standing balsam fir boles was considered to be a result of smoldering after the passage of the fire front, and therefore was not considered in intensity calculations. An average low heat of combustion of 20 000 kJ/kg (8600 BTU/lb) was assumed for all fires.

Discussion and Conclusions

The realities of burning in as explosive a fuel type as the Aubinadong River balsam fir fuel complex, made the completion of the burning program as planned in the initial experimental design, an impossibility. Initial intentions were to conduct a series of ten experimental fires, under a broad range of both spring and summer fire weather conditions. An inability to complete summer fires in the 1978-1980 period, in conjunction with the loss of eight plots in a 1981 escaped fire, resulted in a

Table 5
Fuel consumed by six experimental fires conducted between 1978 and 1982 at the Aubinadong River study area

	Fuel consumption (kg/m²)					
		Surface				
Burn No.	Organic layer	<7.0 cm	≥7.0 cm	Aerial <1.0 cm[1]	Shrubs	Total
1	1.292 (2.77)[2]	0.245	0.049	1.621	0.044	3.251
2	2.058 (3.39)	0.493	0.052	1.776	0.096	4.475
3	0.479 (1.16)	0.489	0.205	1.339	0.138	2.650
4	1.129 (2.50)	0.467	0.153	0.884	0.163	2.796
5	1.523 (3.15)	0.540	0.513	0.924	0.158	3.658
6	0.880 (2.09)	0.515	0.539	1.294	0.170	3.398

[1] Includes all dead balsam fuels ≤ 1.0 cm in diameter plus spruce foliage.
[2] Depth-of-burn (cm).

5-year total of six successful fires at the Aubinadong River site. The range of fire weather conditions, as expressed through the component codes and indices of the FWI System (Table 6) was narrower than initially planned, with fires being conducted only under high to extreme fire danger. Originally it was hoped that experimental fires under lower fire danger conditions would permit the identification of critical Fine Fuel Moisture Code (FFMC) threshold under which effective ignition and fire spread could be sustained. The fire behavior exhibited in the successful experimental fires, however, allows a number of significant conclusions to be drawn.

Spring fires, or those conducted before the flushing of understory vegetation, exhibited spectacular behavior. Total balsam fir crown involvement occurred immediately after ignition (Figures 6(a) and 6(b)) and forward spread rates as high as 80 metres (263 ft) per minute were measured. In addition, balsam fir bark peels readily after mortality, and this fuel is transported in large amounts in the convection column, creating considerable downwind spot fire problems. Heavy water bombers were required to extinguish spot fires up to 0.5 km (0.3 mi.) downwind on all spring fires, and the escape of this type of spot fire in 1981 created the wildfire situation which destroyed a number of plots. Balsam fir aerial and surface fuel consumption is almost complete, with standing tree

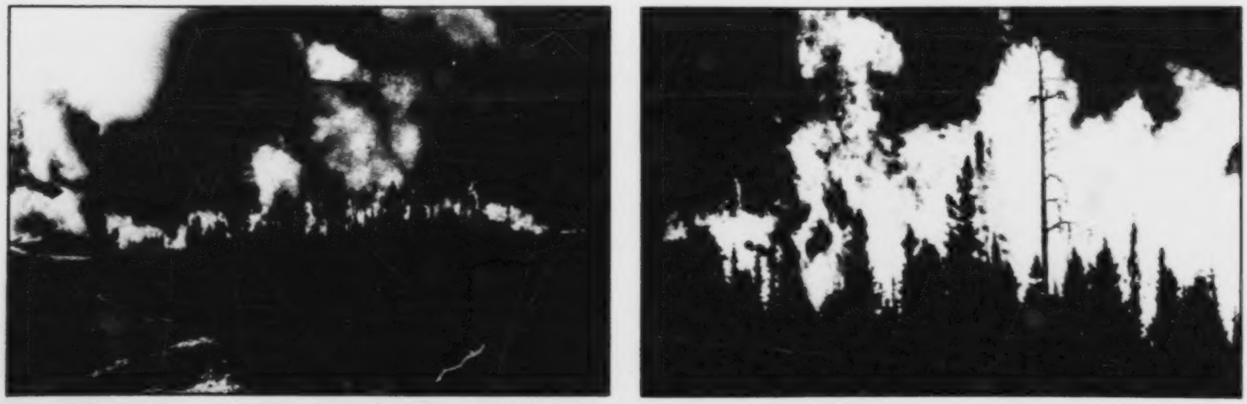

Figure 6(a) and (b). Typical crown fire behavior in dead balsam fir during experimental burning — Aubinadong River.

Table 6

Fire weather conditions, Canadian Forest Fire Weather (FWI) System ratings, and the associated fire behavior characteristics for experimental fires conducted beween 1978-1982 at the Aubinadong River study area

Burn No.	Burn date	1300 hr weather (EDT) Temp. (°C)	RH (%)	Wind[1] (km/h)	FWI system components FFMC[2]	DMC[3]	DC[4]	ISI[5]	BUI[6]	FWI[7]	Rate of spread (m/min)	Total fuel consumption (t/ha)	Frontal fire intensity (kW/m)
1	May 23, 1978	24.0	29	12	91.6	25	55	9.5	25	15	54.1	32.5	58 648
2	May 25, 1978	27.5	34	7	93.1	36	70	9.1	36	17	18.3	44.8	27 298
A[8]	June 6, 1979	20.0	39	15	88.9	21	105	7.7	28	13	—	—	—
B[8]	July 18, 1979	25.0	31	12	91.3	46	173	9.2	55	22	—	—	—
3[9]	May 17, 1981	13.0	34	18	88.1	29	97	8.1	32	15	15.2	26.5	13 462
4	May 25, 1982	27.0	26	14	92.9	46	136	12.6	50	26	82.0	28.0	76 443
5	June 6, 1982	26.5	32	16	91.6	49	185	11.7	59	26	—	36.6	—
6	June 27, 1982	23.0	49	9	87.0	32	270	4.5	50	12	11.5	34.0	13 048

[1] As measured at a height of 10 m in the open or level terrain.

[2] Fine Fuel Moisture Code — a numerical rating of the moisture content of litter and other cured fire fuels.

[3] Duff Moisture Code — a numerical rating of the average moisture content of loosely compacted organic layers of moderate depth.

[4] Drought Code — a numerical rating of the average moisture content of deep, compact, organic layers.

[5] Initial Spread Index — a numerical rating of the expected rate of fire spread (combines FFMC and Wind).

[6] Buildup Index — a numerical rating of the total amount of fuel available for combustion (combines DMC and DC).

[7] Fire Weather Index — a numerical rating of fire intensity (combines ISI and BUI) that is used as a general index of fire danger.

[8] Incomplete burns.

[9] Escaped fire.

boles smoldering long after the passage of the fire front (Figure 7). Fuel arrangement did not seem to be a critical factor in spring fires in this fuel type — fires behaving explosively regardless of whether balsam fir crowns were intact (as in Burns 1 and 2 in 1978), or largely on the ground (as in Burns 4 and 5 in 1982). Dead balsam fir fuel consumption is strongly dependent on the quantity of fuel present on site, rather than on fuel dryness as reflected by the fuel moisture codes of the FWI System. Dead balsam fir boles and crowns, having cured while standing for a number of years, had moisture content values low enough to make virtually the whole tree available for combustion. In comparison, most fires in living conifer forests consume only foliage. Samples taken before each experimental fire indicated dead balsam fir moisture contents of 5-10 percent, 15-20 percent, and 30 percent for fine fuels, medium-sized branches, and tree boles, respectively.

In the first few years following defoliation and mortality, summer fires, occurring after understory flushing, spread very slowly if at all. Incomplete Burns A and B,

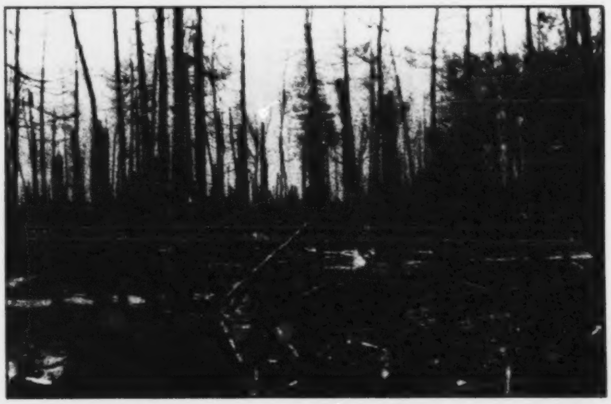

Figure 7. Postfire view — note consumption of dead balsam fir boles.

conducted in 1979 under reasonably severe summer fire weather conditions, failed to spread continuously. With crown defoliation and the subsequent opening of the tree canopy, understory vegetation proliferates very quickly in this fuel type. This moist green layer restricts any interaction between dry ground and crown fuels, effectively nullifying fire spread. After several years, however, enough dead dry surface fuel accumulates through balsam fir decomposition to overcome this dampening effect of understory vegetation, and summer fires will spread through the fuel complex. Burn #6 is an example of this type of fire.

In summary, the Ontario experimental burning program in budworm-killed balsam fir has definitely shown that forest fire potential is significantly increased for several years following mortality in this fuel type. Defoliation in itself does not constitute cause for concern from a potential fire behavior standpoint, but when repeated defoliation causes widespread balsam fir mortality the potential for explosive fire behavior, and attendant fire control problems, increases dramatically. Each of the six successful experimental fires conducted in this study reached intensity levels well beyond the capability of any forest fire control agency. Crown breakage and windthrow, with resultant fuel complex rearrangement and increased surface fuel loadings, reach a peak 5-8 years after mortality. Summer forest fire potential is greatest during this period, decreasing gradually as balsam fir fuel on the ground begins to decompose and understory vegetation continues to proliferate. Spring fire potential is equally high for at least a decade following mortality, and does not seem to be significantly influenced by stand decomposition.

Acknowledgments

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Literature Cited

Baskerville, G.L. 1975. Spruce budworm: Super silviculturist. For. Chron. 61:138-140.

Byram, G.M. 1959. Combustion of forest fuels. Pages 61-89 *in* K.P. Davis, ed. Control and use. McGraw-Hill, New York.

Canadian Forestry Service. 1984. Tables for the Canadian Forest Fire Weather Index System. Can.For. Serv., Ottawa, Ont. For. Tech. Rep. 25 (4th ed.).

Carlson, C.G.; Fellin D.C.; Schmidt, W.C. 1983. The western spruce budworm in Northern Rocky Mountain Forests: A review of ecology, insecticidal treatments, and silvicultural practices. Pages 76-103 *in* J. O'Loughlin and R.D. Pfister, eds. Proc. Symposium Management of Second-Growth Forests: The State of Knowledge and Research Needs, May 14, 1982. University of Montana School of Forestry, Missoula, MT.

Chapman, L.J.; Thomas, M.K. 1968. The climate of northern Ontario. Can. Dept. Trans., Toronto, Ont. Climat. Studies No. 6.

Cottam, G.; Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

Flieger, B.W. 1970. Forest fire and insects: The relation of fire to insect outbreak. Proc. Ann. Tall Timbers Fire Ecol. Conf. 10:107-114.

Furniss, R.L.; Carolin, V.M. 1977.Western Forest Insects. U.S. Dep. Agric., For. Serv., Washington, D.C., Misc. Publ. No. 1339. 654 p.

Graham, S.A. 1923. The drying balsam fir and spruce in Minnesota. Univ. Minn., Agric. Ext. Div., St. Paul, Minn. Spec. Bull. 68. 12 p.

Hansen, H.L.; Krefting, L.W.; Kurmis, V. 1973. The forest of Isle Royale in relation to fire history and wildlife. Univ. Minn., Agric. Exp. Stn., St. Paul. Tech. Bull. 294. 43 p.

Howse, G.M.; Harnden, A.A.; Sippell, W.L. 1973. The 1972 spruce budworm situation in Ontario. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. Inf. Rep. O-X-173. 39 p.

Kent, S.W. 1978. Estimating crown fuel component weights of spruce budworm-killed balsam fir in northeastern Ontario. B.Sc.F. Thesis, Univ. Toronto, Ont. 58 p. + Appendices.

Prebble, M.L. (ed.). 1975. Aerial control of forest insects: A review of control projects employing chemical and biological insecticides. Can. For. Serv., Ottawa, Ont. Misc. Publ. 330 p.

Rothermel, R.C. 1972. A mathematical model for predicting fire spread in wildland fuels. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn. Ogden, Utah. Res. Pap. INT-115. 40 p.

Rowe, J.S. 1972. Forest regions of Canada. Can. For. Serv., Ottawa, Ont. Publ. No. 1300.

Stocks, B.J. 1977. Fire behavior research in Ontario. Fire Manage. Notes 38(2):9-11, 19.

Walker, J.D.; Stocks, B.J. 1975. The fuel complex of mature and immature jack pine stands in Ontario. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. Inf. Rep. 0-X-229. 19 p.

Van Wagner, C.E. 1968.The line intersect method in forest fuel sampling. For. Sci. 14:20-26.

Forecasting Growth and Yield of Budworm-Infested Forests. Part I: Eastern North America

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Procedures used to forecast growth of eastern spruce-fir forests are reviewed. Methodology has evolved continuously since the early 1900s, from normal and empirical yield tables, through a period of widespread reliance on remeasured CFI plots, to the simulation models used today. Scientific studies of growth, yield, and budworm-caused mortality have been available for decades, but were not generally applied until incorporated into simulation models which include dynamic representations of the manager's decision environment.

Retrospective simulations of forest development illustrate that uncontrolled budworm outbreaks obscure the classic volume-over-age yield relationship to such an extent that conventional yield tables become useless. However, if budworm-caused growth reduction and mortality are explicitly included, yields can be predicted accurately with models driven entirely by age-dependent functions. The once-common procedure of extrapolating past periodic annual increments, without considering the age structure of the forest, led to overly optimistic forecasts and has been replaced by models based on age.

Analyses of historical development and predictions of the long-term impact of the current outbreak demonstrate that the spruce budworm exerts a controlling influence on yield of eastern spruce-fir forests. Large-scale outbreaks not only cause major losses of growth and mortality, but also create severely unbalanced age structures that prevent growing stock from being regulated.

Les façons de prédire la croissance des forêts d'épinette et de sapin de l'Est sont examinées. Depuis le début du siècle, les méthodes ont sans cesse évolué; elles se sont d'abord fondées sur des tables de production normales et empiriques, puis, pendant une certaine période, sur les parcelles remesurées de l'inventaire des forêts du Canada et enfin sur les modèles actuels de simulation. L'étude scientifique de la croissance, de la production et de la mortalité causée par la tordeuse a fourni, depuis des décennies, des résultats qui n'ont pas été généralement utilisés avant leur incorporation dans les modèles de simulation qui comportent des représentations dynamiques de l'environnement décisionnel des aménagistes.

La simulation à rebours de la croissance forestière montre que les infestations non réprimées de la tordeuse obscurcissent la relation classique de la production en volume en fonction de l'âge, à un point tel que les tables traditionnelles de production deviennent inutilisables. Toutefois, si l'on tient compte de façon explicite du ralentissement de la croissance et de la mortalité causés par la tordeuse, on peut prévoir fidèlement la production grâce à des modèles gouvernés entièrement par des fonctions dépendantes de l'âge. Autrefois, il était commun d'extrapoler la croissance annuelle périodique antérieure sans égard à la répartition des classes d'âges de la forêt, ce qui a mené à des prévisions excessivement optimistes. Depuis, on utilise des modèles fondés sur l'âge.

Les analyses des antécédents du développement et les prédictions des répercussions à long terme des infestations actuelles montrent que la tordeuse limite la production dans les forêts d'épinettes et de sapins de l'Est. Les infestations généralisées ne causent pas seulement des pertes importantes, par réduction de la croissance et mortalité, mais elles déséquilibrent gravement la répartition des classes d'âge, de sorte qu'on ne peut plus régulariser le matériel en croissance.

Introduction

Until the mid-1970s, forecasting yield of the spruce-fir forests in eastern North America received little attention. In a comprehensive survey conducted only 5 years ago, Field (1980) found that none of Maine's large spruce-fir landowners used yield tables or equations.

Why was yield forecasting not done? Did foresters believe that existing yield tables (e.g.: Meyer 1929; Westveld 1953a; Page and van Nostrand 1973; Ker 1976; Bailey and McNally, 1980[1]; Brewitt 1971; Johnson 1976; Schiltz 1978) were inadequate, or was there simply no need for it? The answer requires a thorough understanding of how the eastern spruce-fir forest and its associated industries have developed over the last 80 years, and involves the spruce budworm (*Choristoneura fumiferana*) to a significant extent. This paper attempts to put historical efforts at yield prediction into perspective, and describes how traditional methods (yield tables) have evolved into the simulation models used today.

Effect of the Budworm on Forest Development and Structure

Unlike its western relative, the spruce budworm is a major tree killer that affects enormous areas at once. During an outbreak, the overriding concern is not on predicting yield, but mortality. Vulnerability of the principal budworm host species (*Abies balsamea*, *Picea rubens*, *P. glauca*, and *P. mariana*) to mortality during the three outbreaks of this century (ca. 1910-20; ca. 1945-55; ca. 1970 to the present) has been studied extensively; see MacLean (1980, 1985) for comprehensive reviews of this literature. This paper focuses on how these results have been adapted into predictive models.

Uncontrolled budworm outbreaks also have another less obvious, but in the long run, much more important effect on yield of eastern spruce-fir forests. When the budworm kills mature trees over large areas in a short time, it makes an indelible imprint on the age structure of the forest. Within a decade, a mature forest characterized by an abundance of merchantable trees is replaced by a new forest dominated by regeneration. As the following discussion illustrates, the budworm's control over the age structure literally governs how much merchantable fiber the affected forest can produce on a sustainable basis.

The budworm's influence on the age structure of stands has been well described by Baskerville (1975) and Mott (1976), but the relationship of these stand-development patterns to forecasting yields of forests has received less attention. This section attempts to link historical growth and yield information with the development of the spruce-fir forest created by the widespread outbreak of 1910-20. The fate of this forest is largely determined by the performance of a single age class: trees which originated, or were released, during the decades surrounding this outbreak, and which now comprise virtually all spruce and fir harvested in eastern North American forests.

1910-20 Outbreak

Although exact figures are not available, between one-half and two-thirds of the eastern spruce-fir forest probably was killed by the budworm and regenerated between 1910 and 1920. Mortality in Maine alone was estimated at over 27 million cords (69 million m^3), with up to 90 percent mortality recorded in some townships (Weed 1977). Similar devastation was reported throughout Quebec and New Brunswick (Swaine and Craighead 1924; Tothill 1919). When Meyer (1929) conducted field work for his red spruce yield tables during the 1920s, he found extensive damage throughout Maine and northern New Hampshire. Mortality and growth reduction were so pervasive that very few "normal" (fully stocked) stands were located, and adjustments to the existing stand structures were required. To quote Meyer: "For each affected plot the diameters were revised so that reduction in diameter due to the damage was eliminated and the tallies were corrected so as to include trees which were killed by the bud worm (*sic*) and which might have lived had they not been attacked."

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[1] Bailey, R.E.; McNally, R.D. 1980. Revised softwood yield tables for Nova Scotia. Unpublished draft, Nova Scotia Dep. Lands and Forests. 27 p. + Appx.

Post-Outbreak Forest — 1925-1940s

By all accounts, the 1910-20 outbreak left the eastern spruce-fir forest depleted. The post-budworm forest was characterized by two broad age classes: remnants of virgin stands that had survived the budworm outbreak and earlier sawlog cuttings, and a new age class that was regenerated and released when the overstory was killed. Surviving merchantable trees were scattered throughout two-storied stands, which apparently were quite understocked by today's standards. In 1933, Sewall estimated that spruce-fir stocking on 3.4 million acres (1.38 million ha) in northern Maine averaged 3.24 cords (8.26 m^3) per acre — about one-third of today's value. By the 1930s, cutting operations had to cover increasingly larger areas just to meet a total harvest that was also declining due to the Depression. From 1936 through 1938, Great Northern Paper Company's harvesting operations averaged 5.1 cords (13 m^3) per acre (Hilton 1942) — an extraordinary figure compared to today's yields which average perhaps 5 times this volume.

Not only were the post-budworm stands understocked, but the surviving trees grew slowly. Many succumbed to windthrow (Sewall, 1933[2]); others took decades to recover from severe topkill (Conlon 1980; Baskerville and MacLean 1979). Budworm devastation apparently was so widespread that Meyer's (1929) normal yield tables, which apply to fully stocked stands, became obsolete (temporarily, as we shall see) almost before their publication. As a result, the U.S. Forest Service initiated a study to develop empirical tables that would more accurately describe yields of the post-budworm forest.

Beginning in 1924, Marinus Westveld established a network of plots in cutover (and probably budwormed) stands throughout northern New England. Instead of age and site index, plots were stratified by the time elapsed since cutting and forest type. Two versions of these tables were published: the first (Westveld 1941) was based on the original data; the second (Westveld 1953a) included an allowance for changes in density based on remeasurement of a portion of the original sample. Neither publication mentioned budworm effects, although concern over the 1940s outbreak reaching Maine was certainly evident (Westveld 1946; McLintock 1947 and 1949).

Westveld's yields were substantially lower than Meyer's. For example, Westveld (1953a) predicts a pure spruce-fir stand of average density would yield about 2070 total cubic feet per acre (144.8 m^3/ha) 60 years after cutting, whereas Meyer's tables predict 4780 cubic feet per acre (344.5 m^3/ha) for site index 50 at the same age. This difference is due in part to the greater density of Meyer's stand (1155 trees per acre) compared to Westveld's (555 trees per acre). However, when one adjusts for higher density using Westveld's procedure, one still predict yields of only 2380 cubic feet per acre (166.5 m^3/ha), less than half of Meyer's value. Clearly, stand structures were different. Westveld's cutover stands must have had a higher percentage of small-diameter trees, whereas Meyer's tables reflect a preponderance of stems in the larger, merchantable diameter classes.

The widely dispersed cutting operations carried out during the 1930s and 1940s removed the outbreak survivors, giving full occupancy of the site to well-developed advanced regeneration that had become established before 1910. Harvests made during the three-decade post-budworm period were, in effect, the final removals in an unintentional application of the shelterwood silvicultural system. After cutting, these stands became quite similar in structure to those that had been completely killed by the budworm and regenerated. This further homogenized the age structure of the entire forest, and exacerbated the imbalance created by the 1910-20 outbreak.

1950-1970 — The Ingrowth Period

By the 1950s, surviving trees that were merchantable during the 1910-20 budworm outbreak became less common, and harvesting operations began to shift to younger stands that survived the outbreak in the sapling stage. At the same time, a heightened interest in growth of spruce-fir forests, coupled with rapidly advancing mensurational practice, led to widespread establishment of permanent, remeasured plots to monitor changes in the resource. Beginning in the early 1950s, large-scale inventories were conducted in Maine by the U.S. Forest Service (Ferguson and Longwood 1960) and in New Brunswick by the Provincial Government (N.B. Dept. Lands and Mines 1958). Large industrial landowners also established systems of continuous forest inventory (CFI) plots (e.g., Letourneau 1966; Bickford et al. 1961; Safford 1968) to provide growth data for management. Plots were normally stratified by forest types in an attempt to lend more general application to the results. Bickerstaff and Hostikka (1977, p. 5-9) summarized the evolution of this method as it was applied throughout Canada. Permanent plots were also used by research agencies to monitor natural stand development and response to various silvicultural treatments in Maine (McLintock 1954; Hart 1956; Solomon and Frank 1983) and northwestern New Brunswick (Vincent 1955; Baskerville 1960; Croome 1970; Hughes 1976).

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[2] Sewall, J.W. 1933. Report on the timber and pulpwood resources of Maine as made under instructions from Mr. Frank H. Holley, State Tax Assessor, 1933. Unpubl. rep. on file at J.W. Sewall Co., Old Town, ME. 116 p.

As information from remeasured plots began to accumulate, it became apparent that an unprecedented phenomenon was underway. The budworm-origin age class was rapidly reaching merchantable size, as evidenced by high rates of ingrowth. Unlike the old-growth stands, which had a distinctly irregular, two-storied structure, these new age classes tended to follow the classic even-aged pattern quite closely. Density was commonly several thousand stems per acre, mostly small-diameter trees on the threshold of merchantable size. Since this age class had become the dominant one, occupying perhaps two-thirds of the softwood forest, growth over the entire resource rose dramatically. Studies reported annual growth rates from 30 to 60 cubic feet per acre (2 to 4 m^3/ha), several times that predicted by Westveld's tables.

Rapid growth continued through the 1960s. The best-stocked stands began to yield volumes remarkably close to those predicted in Meyer's (1929) tables. This development seems ironic, since Westveld's empirical tables had recently been published and were regarded as the more applicable ones. These unprecedented high yields were achieved because budworm-caused mortality, which reduces future yields significantly in immature stands (Baskerville and MacLean 1979), did not occur over most of Maine or New Brunswick. In New Brunswick, much of the infested forest was protected as this age class passed through the ingrowth stage; in Maine, these stands escaped attack because the outbreak did not develop over most of the state.

The unexpectedly high growth rates were at first accompanied by only modest increases in the harvest, and the standing inventory increased significantly. A general belief that the resource was underutilized developed, and major expansions in spruce-fir based industries ensued on both sides of the border to capture this apparent surplus. After nearly two decades of relatively stable growth, managers apparently felt confident in increasing their allowable cuts to levels nearly equal to growth rates observed on their CFI plots. The possibility that this was only a temporary, nonsustainable phenomenon, due to a seriously imbalanced age structure with much of the forest in the rapidly growing 40-60-year age classes, apparently was not considered seriously.

Forecasts made during this boom period were little more than trend-line extrapolations of past growth rates. In their report on the first U.S. Forest Service resurvey of Maine, Ferguson and Kingsley (1972, p. 68) presented several 30-year forecasts based on the assumption that net growth would actually increase in the future. From 1970 to 2000 the softwood inventory (over 80 percent of which is spruce-fir) was predicted to rise from 14.7 to 18.7 billion cubic feet (416.3 million to 529.5 million m^3) in the presence of a predicted 2.5-fold expansion in the harvest by the year 2000. Ferguson and Kingsley (1972, p. 13) did observe that ingrowth, which comprised 63 percent of the total net growth of spruce-fir between 1959 and 1971, was exceptionally high "as a result of recovery from the spruce-budworm epidemic around 1920." However, the possibilities that these high ingrowth rates were evidence of a seriously unbalanced age structure, and that they might not be sustainable, were not addressed.

Simulation of Historical Development

To illustrate these dynamics in more quantitative terms, several simulations of historical stand development were carried out. Stands with identical species composition (54 percent fir, 46 percent spruce) were "regenerated" at different times in the past, and "grown" forward to 1970 at 69 percent of Meyer's (1929) rates for site 50. Fir yields were reduced for natural old-age mortality beyond age 70 to reflect the normal breakup and decline of this species at old ages (Baskerville 1965). Decades of stand origin were selected to give the range in age classes that Westveld would have faced when constructing his empirical tables, and those that are common today. A simulated uncontrolled budworm outbreak was begun in 1910; tree mortality rates increased with age and were higher for fir than spruce, in accord with MacLean's (1980) review. The only difference among the development curves was the timing of the budworm attack relative to the age or stage in development of each stand. Simulations were carried out using the Green Woods model (Seymour et al. 1985), which is described in a later section.

Simulated development of each age class is shown in Figure 1. Stands begin to accumulate merchantable volume at age 25 and grow rapidly for about three decades, or until attacked by the budworm. The 1815-origin stand reaches a peak yield ca. 1890 at age 70 and declines naturally for two decades before the 1910 budworm attack. Other stands originating before 1900 are budwormed at much earlier, more vigorous stages in development, ranging from age 20 (1890 origin) to 50 (1860 origin). Stands originating from 1900 on are unaffected by the outbreak, and grow along parallel tracks a decade apart until 1970.

Variations in age at the time of attack produce many interesting, contrasting stand responses which illustrate the historical trends discussed above. Simulated mortality and growth reduction increase with age; the 1890-origin stand merely stagnates for a 10-year period, whereas the 1815- and 1860-origin stands lose nearly half their volume. The post-outbreak response is even more variable. The 1815-, 1860- and 1870-origin stands end the outbreak (ca. 1920) with about the same volume, but respond quite differently due to their ages. The 1880- and 1890-origin stands are less

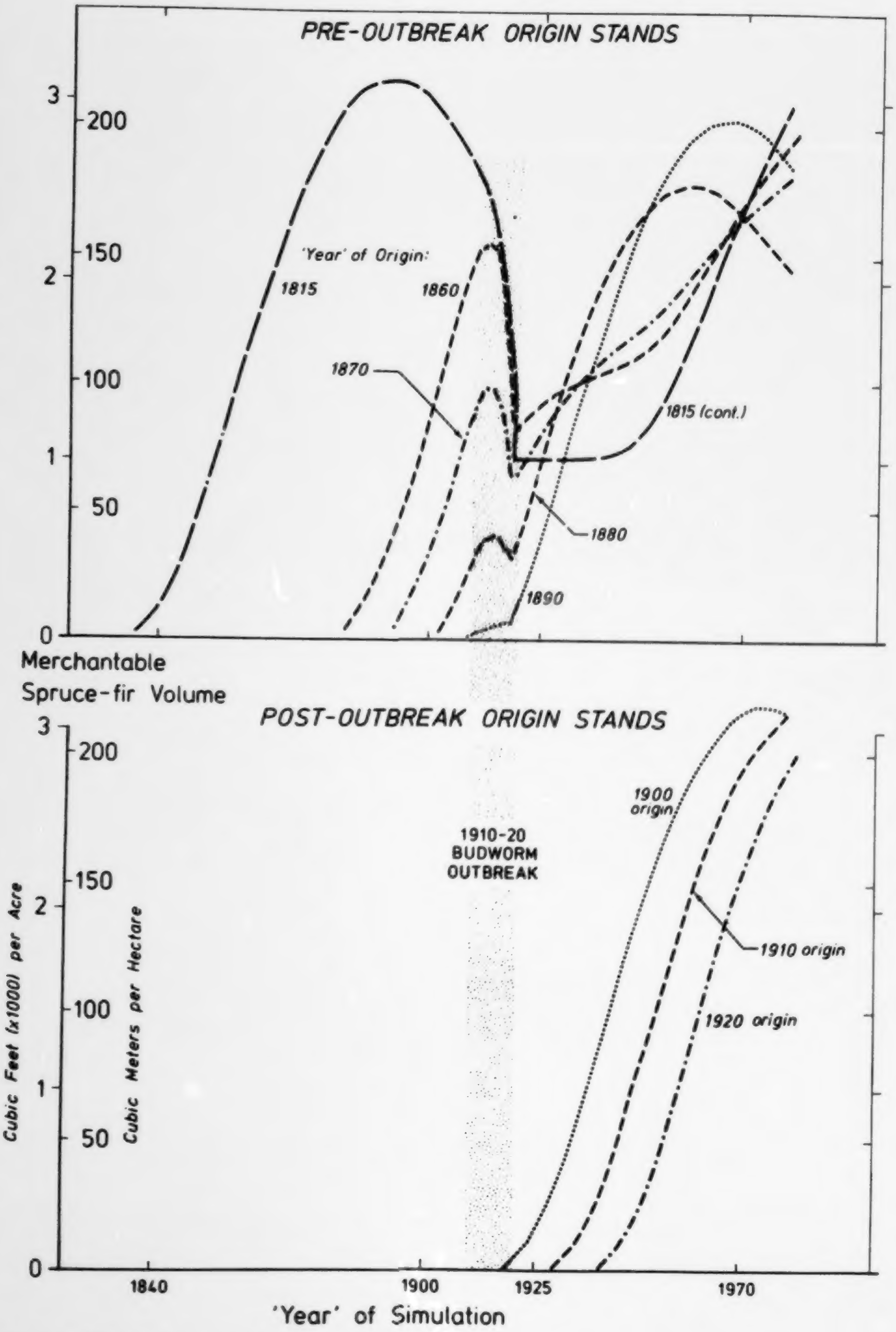

Figure 1. Effects of the 1910-20 budworm outbreak on development of mixed red spruce-fir stands originating between 1815 and 1920. (Simulated by the Green Woods model using 69 percent of Meyer's (1929) yield for site 50).

affected, and recover more abruptly. About 1930, three different age classes (1860, 1870 and 1880 origin) all have virtually the same volume, because of largely coincidental combinations of original (pre-outbreak) stocking, mortality, and response.

This situation is quite temporary, however, and the 1880- and 1890-origin stands quickly surpass the older age classes. Interestingly, this produces a situation from the 1930s through the 1950s where standing volume is actually negatively correlated with age. Stands attacked at age 40 or older apparently never recover from the understocking effects until the new age class that originated within the stand during the outbreak begins to gain volume in the 1950s. Stands originating after 1900 survive the outbreak without being understocked, and as a result, surpass the older stands in yield by a substantial margin by about 1960.

Given this situation, it is not surprising that conventional yield tables were not used during the post-outbreak era. Budworm had obscured the normal even-aged development patterns to such an extent that age alone was meaningless as a predictor of standing volume. However, it must also be emphasized that these simulated trends, which appear to be consistent with the observed development of the post-outbreak forest, were generated by a model that is driven entirely by age-dependent functions, including a simple normal yield table. Apparently, yield tables are appropriate as long as the negative effects of the budworm are included.

To reinforce this point, the simulated 1925 per-acre volumes (from Figure 1) in each of the six stands that originated between 1860 and 1910, inclusive, were compared with those in Westveld's tables for similar stand conditions. Except for the yields of the first two age classes (10 and 20), which in Westveld's tables represent volumes of residual trees left after commercial clearcutting operations, the correspondence is remarkable (Figure 2). Apparently Meyer's and Westveld's tables, which have always been considered to be so discrepant, are actually consistent when budworm effects are taken into account. The classic sigmoid growth curve defined by Meyer's tables appears to be generally applicable, especially if reduced for below-normal stocking. Westveld's empirical tables clearly represent a special case for an understocked, post-budworm forest.

A similar comparison was made between the simulated 1970 yields and those compiled in the 1970 U.S. Forest Survey of Maine (D. Seegrist, unpublished data). Here, the correspondence is not as good, especially in the 50-70-year age classes (Figure 3), where Meyer's curves overpredict actual volumes by over 1000 cubic feet per acre (70 m^3/ha). The overall pattern is quite similar, however; shifting the simulated yields 20 years to the right (in effect, increasing the ages at which yields are reached) produces close agreement. Many possible reasons could account for this discrepancy. Suppression from competing vegetation early in the life of existing stands may have delayed their development.

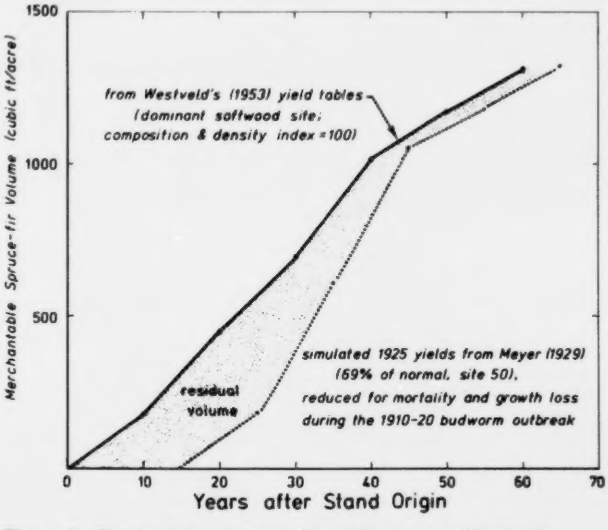

Figure 2. Comparison of spruce-fir yield between Westveld's (1953a) empirical tables (dominant softwood sites, composition and density index = 100) and Meyer's (1929) normal tables adjusted for understocking and mortality from the 1913-19 budworm outbreak.

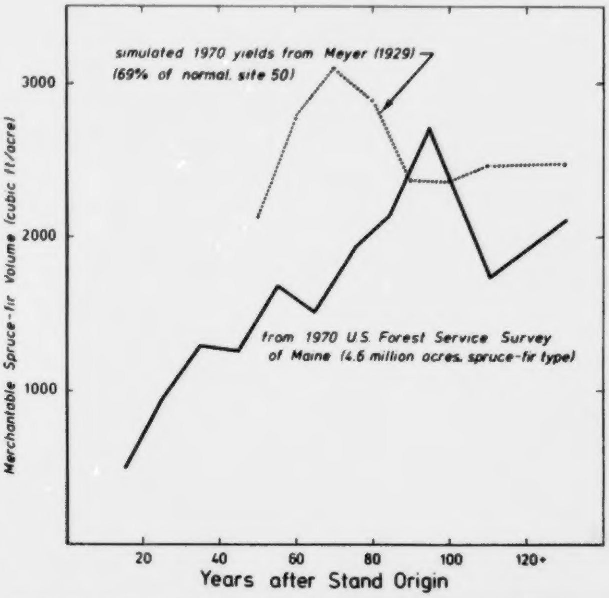

Figure 3. Comparison of yields simulated by the Green Woods model (69 percent of Meyer, site 50, budworm outbreak during 1910-20) with actual volumes per acre by ten-year age classes observed in the 1970 Forest Survey of Maine. (Unpublished data provided by Donald Seegrist, USFS, NE Forest Experiment Station, Broomall, PA.)

Also, harvests may have been allocated preferentially to stands with higher-than-average volumes at a given age, such that those remaining exhibit below-average yields.

1970s — The Forest Declines Again, the Budworm Returns

The final chapter in the development of the budworm-origin age class is still being written, but certain trends are evident. Beginning about 1970, ingrowth began to fall off and mortality of the smaller-diameter, lower crown classes increased. For a time, reduced ingrowth was offset by greater accretion (survivor growth), so no perceptible change in net growth was observed. However, instead of continuing to grow into merchantable size, small trees began to die in large numbers from natural suppression. This was the first conclusive evidence that the all-aged paradigm advocated by some spruce-fir silviculturists of the post-budworm period (Westveld 1953b) was suspect. In essence, over half the forest was maturing in one great wave. This development of even-aged stands over large areas is an event none of the foresters active in Maine in the 1940s expected (T.F. McLintock, personal communication, 1984).

In the mid-1970s, an extensive budworm outbreak developed, and has since infested virtually all susceptible forest type in the region. Studies established to monitor growth reduction and tree mortality from the outbreak (Lawrence and Houseweart 1981; Schiltz et al. 1983; Clowater and Andrews 1981; Nova Scotia Dept. Lands and Forests 1980) confirm that yet another era in forest development is unfolding. The current outbreak, and unprecedented harvest levels resulting from recent industrial expansions, have accelerated the inevitable maturation of the 60-80-year-old stands that originated during the previous outbreak. Contrary to earlier predictions of continued growth, forecasts made with a newly developed methodology (described below) are ominous at best. Unquestionably, the standing inventory is once again in decline, and profound structural changes in the resource are occurring.

What Went Wrong?

The preceding discussion leads to some interesting observations and lessons about the relationship of forest development and yield forecasting. Since the beginning of forestry in the spruce-fir region, the basic ecological processes driving patterns of stand development in this forest type have not changed, yet our collective impression of how much the forest will yield has gone through a continuing, cyclical evolution. Practitioners in each period were obviously influenced by the common stand structures of the time, and tended to believe that the forest would "always be this way." Although changes are obvious given several decades of hindsight and information, they occurred slowly and imperceptibly. Indeed, the forest remained in one developmental stage for a length of time that spanned much of a forester's active career. By the time sufficient knowledge and understanding had accumulated about how the common stand structures would grow, the forest matured and a new kind of stand, with no recent historical precedent, became the norm. Thus, at the time, the yield forecasting procedure common during the 1950s and 1960s — extrapolating past periodic annual increments from CFI plots — seemed eminently logical.

The fallacy in this approach was its failure to foresee the inevitable changes that were being driven by the unbalanced age structure of the forest. Failure to perceive the underlying, age-related dynamics was perhaps more pronounced in Maine than Canada. Indeed, Bickerstaff (1949) accurately foresaw many of the problems associated with the then-common approaches to growth forecasting, but his prophetic remarks apparently went largely unheeded. One reason why the situation was perhaps more obscured in Maine is due to the higher red-spruce composition of Maine's forests. Because this species is inherently longer-lived and more resistant to budworm mortality than its common associate, balsam fir, a wider variety of stand development patterns exists in Maine than in the more northerly regions where balsam fir predominates (Mott 1980).

For the purpose of predicting yield of the future forest, traditional historical growth data have proven to be of little value. The basic problem is that remeasured plots, when established by sampling schemes heavily weighted toward existing merchantable stands, reflect an empirical "average" of stand structures that no longer exists in the forest as a whole by the time the information is analyzed. Sampling designs used for estimating volumes accurately have proven to be far from ideal for predicting growth and future development. In effect, plots were put in areas were wood was present at the time, not where it was expected to be 30 years later. As a result, a new approach to inventory and yield prediction has evolved. Inventories are designed primarily to describe resource parameters such as age structure and regeneration conditions that are required for forecasting future harvest levels. Traditional objectives such as estimating the present-standing inventory or documenting historical development receive less emphasis.

Yield Forecasting with Models

As awareness of the shortcomings of CFI plots grew during the 1970s, it became apparent that a new approach to forecasting growth and development of spruce-fir forests was needed. Independently on both sides of the border, models which explicitly take into account the age structure of the forest have been created, tested, modified, and widely applied. The remainder of this paper will discuss these: WOSFOP (Wood Supply and Forest Productivity model, Hall 1978), which has been under continuous development by New Brunswick scientists since the mid-1970s, and the Green Woods model (Seymour et al. 1985) created in 1980 by scientists at the University of Maine as part of a CANUSA-sponsored IPM demonstration project. Although relatively new, both have enjoyed extraordinarily wide use since their development.

Both models were designed to make forecasts at the scale of the entire forest or sustained yield land area, not for individual stands. In essence, they are forest dynamics models, much like harvest scheduling models without an optimization component. Out of necessity, they are intended to give forest managers the "big picture" of the probable outcome of forest dynamics by rapidly predicting the effects of various harvesting, protection, and silvicultural strategies on future wood supplies. This is done at some sacrifice in detail, but this is not considered a weakness. The spruce budworm creates problems that must be dealt with on a large scale, typically an entire forest or region. Predicting effects on individual stands, although potentially useful in designing silvicultural tactics during an outbreak, has not been the principal concern of managers.

Both WOSFOP and the Green Woods model characterize the forest by distributing its area into relatively broad strata based on age or stage of development. This initial structure is then projected ahead in time using simple growth or yield functions, management is applied through various harvest and treatment rules, and regeneration occurs. An interesting feature of both is that yield functions are built and modified primarily by the user; default processes are discouraged or nonexistent. This places a heavy burden on users, yet these models have been well accepted. Apparently, managers are more comfortable with this approach, because they, not the model-builder, make the essential assumptions.

Neither model simulates budworm population dynamics. Budworm effects are limited to mortality and growth reduction. However, it is interesting that both models were originally developed to address resource-level protection problems posed by the current budworm outbreak.

Despite their similarities, Green Woods and WOSFOP differ in several ways, due to the purposes for which they were designed. The following discussion outlines the mechanics of how each works.

The Green Woods Model

In the Green Woods model, the forest is divided into softwood and mixedwood forest types, which are each broken down by the percentage of budworm host species (spruce and fir) and one-year age classes. Each of these strata are then further subdivided by their protection status if a budworm outbreak is underway. On lands defined as protected, no budworm-caused tree mortality occurs. This simulates the operational concept of a long-term protection zone, where treatments are applied as needed to prevent mortality. On unprotected lands, tree mortality occurs as described below.

Growth and mortality are calculated annually during a simulation, and previous volumes in each stratum are updated. This differs from WOSFOP, in which the entire course of development for each stratum over its entire life is predetermined by a user-specified yield curve. Growth is a function of age, species, and forest type. Meyer's (1929) normal yield tables (merchantable cubic-foot volume) for site index 50 (softwood type) and 60 (mixedwood type) are formulated with a Weibull density function, but any prediction equation with age as the independent variable can be substituted. An optional table look-up is also available for the user to construct his own function if Meyer's curves are found to be too confining. Calibration factors can be used to match virtually any assumed model. A separate function simulates natural (i.e., nonbudworm) old-age mortality of balsam fir, which causes net yield of this species to decline beyond age 70.

To simulate a budworm outbreak, users specify when defoliation begins and how long it is expected to last. When an outbreak is generated, a 6-year tree mortality sequence begins on all lands left unprotected in the simulation. The mortality sequence can begin immediately, or be delayed up to 8 years, after the onset of defoliation. Mortality can vary by species, age, and forest type. Mortality is simulated by removing percentages of the volume from all unprotected age classes; in age classes over 50, area is also removed and "regenerated."

In the first version of Green Woods, budworm-caused mortality was modelled as several reverse-logistic functions of age that were formulated to agree with all previous mortality studies (MacLean 1980). After repeated trials, these functions were discarded mainly because they could not be made to predict the high mortality of red spruce and young fir observed in the current outbreak. In the present version, users specify mortality rates based on the levels expected in their particular infestation. Many foresters unfamiliar with budworm damage were initially uneasy with these demands. However, as their experience in the present outbreak grew, many now prefer this approach. Sensitivity analyses on expected mortality, an inherently uncertain variable, can readily be carried out.

During a simulated outbreak, normal growth rates are reduced to account for the effects of nonfatal defoliation. At the user's option, growth reduction can vary by species, and can occur at different rates on protected as well as unprotected lands.

After harvesting, regeneration can change species composition, forest type, and undergo a "lag," or delay in establishment. Regeneration after budworm mortality is handled differently; attacked stands under age 50 are simply understocked and do not regenerate. Over age 50, new age classes are created in proportion to the mortality of the overstory. Species composition of budworm-caused regeneration remains the same as the parent age class, and does not undergo a lag.

The forest is "managed" by flexible harvesting and protection algorithms designed specifically to replicate the decision process in Maine. When the model was developed, several important questions faced Maine's foresters: How much area must be protected from budworm mortality to allow a certain harvest level to be sustained? How would accelerating the harvest of fir, and switching to more targeted protection programs, affect future wood supplies?

To address these questions, the model was structured so that the proportion of fir in both the total harvest and total area under protection could be varied within feasible limits. Other elements of the harvesting strategy that are specified explicitly are the minimum operable age, relative concentration on the oldest wood, amount to be salvaged from standing dead material, and the allocation to protected or unprotected lands. Harvest levels are specified in terms of merchantable cubic feet only; product or diameter classes are not distinguished.

Protection is simulated by specifying the areas where no budworm-caused tree mortality will take place. Protection can be varied by age class, species, and forest type, to replicate protection programs that are targeted on these components of the resource.

WOSFOP

In WOSFOP, the forest structure is characterized by "development classes" (Clifford 1981). These are similar in concept to Westveld's (1953a) "effective age" classes, in which expected future yield, not actual biological age, is the crucial consideration. Stands that are believed to be at different stages of development, but within a common overall pattern are aggregated into "forest units." These are analogous to the forest types (softwood and mixedwood) used in the Green Woods model, but may number as many as 20 to capture the variability in the forest.

Unique yield curves are specified for each forest unit using a purely empirical approach (Figure 4). Based on information from local inventory plots, users define the ages and corresponding yields at four stages in stand development: when merchantable volume first appears; when net growth and mortality offset each other; when mortality exceeds net growth; and when no merchantable trees remain on the site. The intervening periods correspond roughly to stand establishment, ingrowth and accretion, stagnation, and decline. When the forest is initialized, each development class is assigned to a particular 10-year age class, which positions it at the appropriate point on the yield curve for its forest unit.

Descriptions of the forest units and their respective yield curves are entirely arbitrary, and are chosen to reflect stand units that are developing along similar paths. This feature permits users to "customize" the model to their particular forest. Forest-unit strata are normally determined from cover type maps; sample plots provide the stocking levels and ages used to distribute areas by development classes. The resulting model is extremely flexible. Managers can undertake wood supply analyses for irregular, empirically stocked forest types whose growth and yield patterns have not been studied formally or published.

Unlike the Green Woods model, WOSFOP does not explicitly model budworm-caused tree mortality or

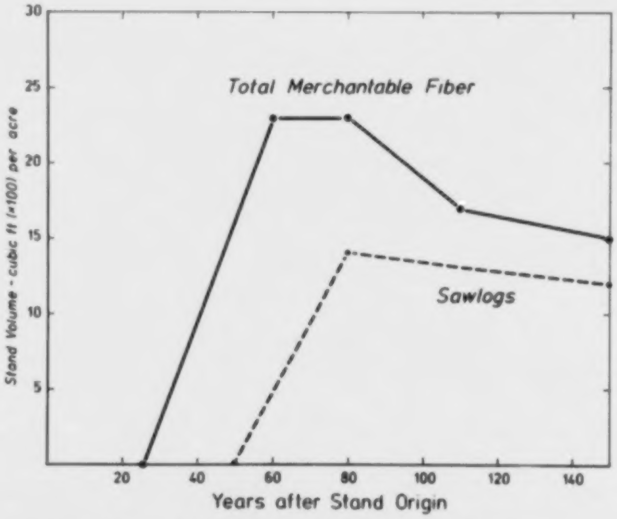

Figure 4. Typical yield curve used in the WOSFOP model. Applies to fir-spruce high-yield forest unit in northwest New Brunswick (adapted from Clifford 1981).

growth reduction. These impacts, if any, are manifested in the yield curves themselves which, by definition, define the net result of both positive and negative growth components. Modeled yields for the various fir-spruce forest units were not reduced for budworm effects. Because the New Brunswick softwood resource has been infested since the 1950s and protected against tree mortality, it was felt that the empirically derived yield curves would already include an appropriate allowance for the budworm in the current forest and would therefore be applicable as long as the future infestation dynamics did not change.

An obvious weakness of this method was that reductions or increases in protection could not be simulated directly. This drawback has recently been overcome by MacLean and Erdle (1984), who developed a method to construct yield curves for unprotected as well as protected and uninfested stands. Budworm-caused mortality and growth reduction are predicted for each forest unit based on its species composition, age, and other factors, and the yield curves are lowered accordingly. The net result is similar to, though perhaps less flexible than, the approach used by the Green Woods model.

Unlike the Green Woods model, regenerated areas in WOSFOP can follow different yield curves than the parent stands. Yields of young stands can either be reduced to simulate poor stocking after harvesting, or increased to model results of silvicultural treatments, such as planting or precommercial thinning. This ability to "manage" the "new" forest at a higher level of intensity than the existing "old" forest is a major advantage for strategic planning, and was the principal motivation in model design (G.L. Baskerville, personal communication). Large-scale silvicultural programs designed to stabilize or increase future wood supplies can readily be simulated.

WOSFOP'S harvesting algorithms are less flexible than those employed by the Green Woods model. Various modifications of "oldest first"-type rules are used. Volumes cut by species, and salvage of budworm-killed timber, cannot be specified directly, except by changing harvest allocation to different stand compositions. One advantage is that yields and harvests can be specified separately for pulpwood and sawlogs.

Model Applications

The Green Woods model was originally developed to predict the impacts of integrated forest management strategies on several demonstration areas established in Maine with funding from CANUSA and cooperation from several large landowners (Mott et al. 1981). A central theme of the Green Woods Project was to test various harvesting and protection strategies that were targeted according to the species composition of stands (Mott 1980; Dimond et al. 1984). The first application of the model was to Maine's entire spruce-fir resource (Seymour et al. 1980)^3 in response to the threatened abandonment of the 1980 spray program. Though this report was never published, it was nevertheless circulated widely and used to plan the U.S. Forest Service's involvement in Maine's annual budworm suppression program (USDA Forest Service 1981). The Green Woods model has since been used extensively by almost all large private spruce-fir landowners in Maine.

Most recently, the model was used as the forecasting tool for an analysis of future spruce-fir supplies in Maine (J.W. Sewall Co. 1983; Edson 1983). This study explored how varying levels of protection against budworm, different harvest schedules, and increased application of silvicultural treatments might affect the long-term sustainability of Maine's spruce-fir based industry. Results showed that no feasible level of protection can avert an eventual shortfall; increasing the area treated helps marginally (Figure 5), but merely postpones the inevitable. Interestingly, the inventory declines even in the hypothetical scenario of no budworm outbreak. Clearly, the unbalanced age struc-

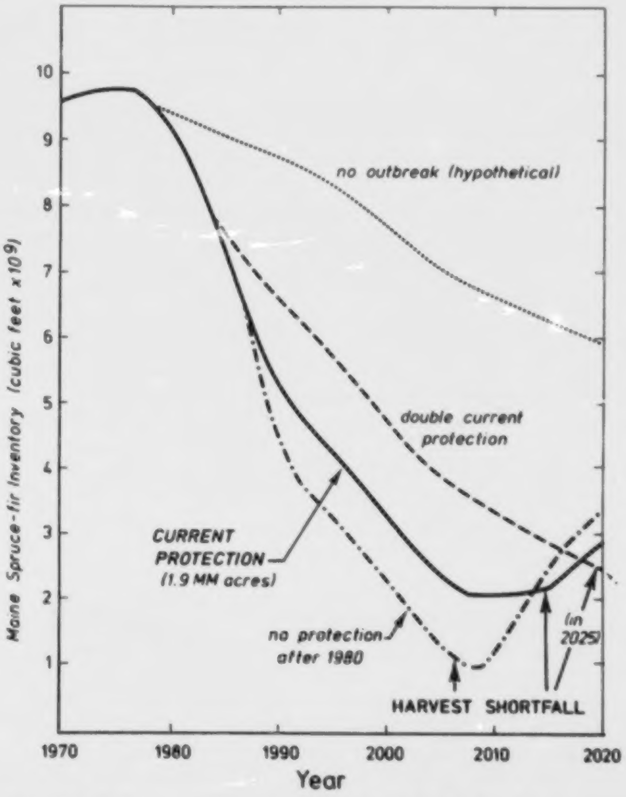

Figure 5. Fifty-year scenarios of Maine's spruce-fir inventory simulated by the Green Woods model (adapted from Sewall Co. 1983).

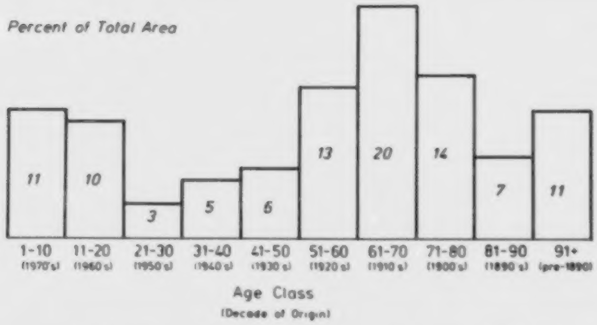

Figure 6. Age structure of Maine's spruce-fir forest, 1980.

ture (Figure 6), and a widespread, severe budworm outbreak have set in motion an inexorable process of inventory decline and structural change in the resource. Lowering the harvest 10 to 25 percent below the current level avoids a shortfall, but obviously does not sustain the present industry without improvements in utilization. These predictions are dramatically at odds with the earlier forecasts of Ferguson and Kingsley (1972), but have been widely accepted as valid by industrial landowners (Yacavone 1983) and outside reviewers (Baskerville 1983a).

A significant weakness of the Green Woods model became evident in the conduct of this study. The basic problem, well articulated by Baskerville (1983a), is that the model deals with "average" conditions over broad age classes. It is not possible to connect simulated harvesting and protection strategies directly with specific geographic areas or stands on the ground. This is an advantage for resource-level analyses (due to its simplicity) but becomes limiting when attempts are made to alter growth rates on particular components of the resource, for example, to predict the response to widespread precommercial thinning or planting programs. Consequently, efforts in Maine have now begun to focus on developing or adapting models with more stand-level detail and the capability to handle the diverse array of existing stand structures. No further development of the Green Woods model is contemplated, although its algorithms for modeling budworm effects and harvesting strategies will likely be retained in any new models.

WOSFOP was patterned after similar models used by Nova Scotia Forest Industries in the late 1960s to forecast the response of various management regimes (G.L. Baskerville, personal communication). In structure, WOSFOP resembles the simple forest submodel that was originally incorporated within a larger, sophisticated model of budworm population dynamics. The budworm model, which has become known as the MFRC-UBC model for its developers at the Maritimes Forest Research Centre and the University of British Columbia (Fisher 1982), was used in a comprehensive analysis of forest protection strategies for New Brunswick (Baskerville 1976). Although not its original purpose, this analysis showed the provincial inventory of spruce-fir to be declining, contrary to earlier predictions made by conventional forest regulation formulae. This unexpected result stimulated further development by the New Brunswick Department of Natural Resources. This work culminated in Hall's (1978) unpublished manuscript which is now cited as the model's seminal document (Cuff and Baskerville 1983).

Hall's (1978) analysis raised serious questions about the value of conventional forest inventory data and allowable-cut calculation methods for predicting future woods supplies. Clifford (1981) further refined the model and applied it to a 1.9 million-acre (769 000 ha) case in northwestern New Brunswick. Although the test was generally successful, sensitivity analyses showed that inventory information was a significant source of uncertainty. Stand descriptions were largely mensurational, and were not well suited to predicting future development.

These efforts raised such concern about future wood supplies in New Brunswick that a major effort to reallocate harvesting licenses on Crown lands and specify management activity levels was undertaken under the direction of Gordon Baskerville, then Assistant Deputy Minister in the New Brunswick Department of Natural Resources. WOSFOP was the primary analytical tool used in this effort, which culminated in 1981. In the process WOSFOP has also been adapted for use by three other provinces and over 20 forest industries (Cuff and Baskerville 1983). New Brunswick has since embarked on a major new forest development survey to improve the data base for further wood-supply work. Software designed to link WOSFOP with the Provincial Geographic Information System is also under active development. The goal is to monitor actual implementation of management programs and to depict spatially the simulated harvesting and protection plans.

Lessons from Model Development and Application

Although both WOSFOP and the Green Woods model have proven to be extremely useful to forest managers, it can be argued that they have performed an even greater service to the science of forecasting yield and budworm damage. By design, these models attempt to capture in one place the complex dynamics of managed, budworm-infested spruce-fir forests. In the process, they have become a focus for all previous

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[3] Seymour, R.S.; Mott, D.G.; Kleinschmidt, S.M. 1980. Future impacts of spruce budworm management - a dynamic simulation of the Maine forest 1980-2020. Green Woods Proj. Unpubl. Rep. 88 p.

scientific studies of growth and yield, stand development, and budworm vulnerability, many of which had gone essentially unutilized for decades.

However, it was probably not the models' characterization of the natural forest dynamics that caused formerly unused results to be applied, but rather the deliberate inclusion of the forest manager's decision processes. For example, neither Meyer's (1929) yield tables nor Craighead's (1924) classic work on budworm-caused red spruce mortality were used until the Green Woods model gave the manager a means of harvesting and protecting forests through simulation as well as growing and killing them. On the basis of this experience, one could argue that unless models include the managerial decision processes, the ecological dynamics and natural constraints on resource productivity will be ignored.

This interface between science and practice appears to be crucial to any model's success (Cuff and Baskerville 1983), and has produced benefits to both sides. By using these models, managers develop a thorough understanding of how the natural processes work and what they can and cannot expect their resource to produce. Scientists gain an appreciation for "what's important" to forest managers, and can structure further research to close critical gaps in knowledge. Experience with these models has identified many weaknesses amenable to further research. Perhaps the greatest source of uncertainty lies in the yield of infested stands that are protected to prevent mortality but still experience chronic, nonfatal defoliation (Baskerville and Kleinschmidt 1981). The other important area of interest is in predicting response of silviculturally treated stands in the "new" forest, which hold the key to wood supplies in the next century.

Conclusions

Retrospective analyses and forecasts of forest response to the current outbreak demonstrate that the spruce budworm exerts an overriding influence on the growth and yield of the spruce-fir forests of eastern North America. Although tree mortality and reduced growth are certainly powerful effects during active outbreaks, the budworm exerts its greatest influence on productivity by controlling the age structure of the forest. By periodically killing trees and regenerating stands over large areas in a very short time relative to economic rotations, budworm outbreaks historically have prevented the eastern spruce-fir forest from being brought under regulation. Even though the budworm itself may not be present for decades, its imprint on the forest, manifested as a distinctly unbalanced age structure, remains for a full rotation after the last tree dies from defoliation.

Large-scale protection programs now in effect over significant portions of the eastern spruce-fir forest not only ameliorate the short-term, stand-level impacts, but in the long run permit forest managers to gain some degree of control over the age structures of their forests (Baskerville 1983b). This latter effect may be the single most important justification for protection and may outweigh the short-term benefits of preventing growth reduction and tree mortality.

Literature Cited

Baskerville, G.L. 1960. Conversion to periodic selection management in a fir, spruce and birch forest. Can. Dept. Northern Affairs and Natural Resources, Forestry Branch, Forest Res. Div., Ottawa, Ont. Tech. Note 86. 19p.

Baskerville, G.L. 1965. Deterioration and replacement in two overmature forest stands. Canada Dept. Forestry, Ottawa, Ont. Publ. No. 1125. 16p.

Baskerville, G.L. 1975. Spruce budworm: super silviculturist. For. Chron. 51:138-140.

Baskerville, G.L. 1976. Report of the task force for evaluation of budworm control alternatives. New Brunswick Dept. Natural Resources, Fredericton, N.B. 210 p.

Baskerville, G.L. 1983a. A critique and commentary on the 1983 supply/demand analysis for the spruce-fir resource of Maine. Available from: Maine Dept. Conservation, Augusta, ME. 56 p.

Baskerville, G.L. 1983b. Approaches to the spruce budworm problem in Nova Scotia and New Brunswick. Pages 73-81 *in* C.J. Sanders and J.R. Carrow, co-chairmen. The spruce budworm problem in Ontario — real or imaginary? Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. COJFRC Symp. Proc. O-P-11. 116 p.

Baskerville, G.L.; MacLean, D.A. 1979. Budworm-caused mortality and 20-year recovery in immature balsam fir stands. Can. For. Serv., Maritimes For. Res. Centre. Info. Rep. M-X-102. 23 p.

Baskerville, G.L.; Kleinschmidt, S.M. 1981. A dynamic model of growth in defoliated fir stands. Can. J. For. Res. 11:206-214.

Bickerstaff, A. 1949. Growth pains. For. Chron. 25:311-314.

Bickerstaff, A.; Hostikka, S.A. 1977. Growth of forests in Canada. Part 1: An annotated bibliography. Can. For. Serv., For. Manage. Inst., Ottawa, Ont. Info. Rep. FMR-X-98. 197 p.

Bickford,C.A.; Longwood, F.R.; Bain, R. 1961. Average growth rates in the spruce-fir region of New England. U.S. Dep. Agric., For. Serv. Northeastern For. Exp. Sta., Upper Darby, PA. Sta. Res. Pap. No. 140.

Brewitt, P.D. 1971. Yield of evenaged spruce-fir in western Maine as influenced by age, site index, and stand density. M.S. thesis, Sch. of For. Resour., Univ. Maine, Orono. 90 p.

Clifford, W.L.T. 1981. Wood supply analysis by simulation. M.S. thesis, Faculty of Forestry, Univ. New Brunswick. 83 p.

Clowater, W.G.; Andrews, P.W. 1981. An assessment of damage caused by the spruce budworm on spruce and balsam fir trees in New Brunswick. New Brunswick Dept. of Nat. Resour., For. Manage. Branch, Fredericton, N.B. 23 p.

Conlon, F.J., Jr. 1980. Analysis of growth responses in released spruces (*Picea rubens* Sarg., *P. mariana* (Mill.) B.S.P.), and fir (*Abies balsamea* (L.)) in Maine. M.S. thesis, Sch. of For. Resour., Univ. Maine, Orono. 63 p.

Craighead, F.C. 1924. Studies on the spruce budworm (*Cacoecia fumiferana* Clem.). Part II. General bionomics and possibilities of prevention and control. Canada Dept. of Agric., Ottawa, Ont. Tech. Bull. 37 (new series). pp. 28-91.

Croome, G.C.R. 1970. A trial of selection management in a fir-spruce-birch forest. For. Chron. 46:317-321.

Cuff, W.; Baskerville, G. 1983. Ecological modelling and management of spruce budworm infested fir-spruce forests of New Brunswick, Canada. Pages 93-98 *in* W.K. Lauenroth, G.V. Skogerboe, and M. Flug, eds. Analysis of ecological systems: state-of-art in ecological modelling. Developments in environmental modelling 5, Elsevier Scientific Publ. Co., New York.

Dimond, J.B.; Seymour, R.S.; Mott, D.G. 1984. Planning insecticide application and timber harvesting in a spruce budworm epidemic. U.S. Dept. Agric., For. Serv., Washington, D.C. Agric. Handb. 618. 29 p.

Edson, D.T. 1983. Spruce/fir supply 1970-2020. Pages 57-63 *in* T.J. Corcoran and D.R. Gill, eds. Recent advance in spruce-fir utilization technology. Proc. of a Symp., 17-19 Aug. 1983, Univ. Maine, Orono, 222 p.

Ferguson, R.H.; Longwood, F.R. 1960. The timber resources of Maine. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Upper Darby, PA. 75 p.

Ferguson, R.H.; Kingsley, N.P. 1972. The timber resources of Maine. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Upper Darby, PA. Resour. Bull. NE-26. 129 p.

Field, D.B. 1980. The economic importance of Maine's spruce-fir resource. Coop. For. Res. Unit, Res. Bull. 2, Sch. For. Resour., Univ. Maine, Orono. (Maine Agr. Exp. Sta. Misc. Rep 227). 34 p.

Fisher, R.A. 1982. Two decades of budworm simulacra. A retrospective view of comprehensive simulation models. Pages 107-111 *in* W.K. Lauenroth, G.V. Skogerboe, and M. Flug, eds. Analysis of ecological systems: state-of-art in ecological modeling. Developments in environmental modeling 5, Elsevier Scientific Publ. Co., New York.

Hall, T.H. 1978. Toward a framework for forest management decision-making in New Brunswick. New Brunswick Dep. Nat. Resour., Fredericton, N.B. Rep. No. TRI-78. 83 p.

Hart, A.C. 1956. Changes after partial cutting of a spruce-fir stand in Maine. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Upper Darby, PA. Sta. Pap. No. 86. 8 p.

Hilton, C.M. 1942. Rough pulpwood operating in northwestern Maine 1935-40. The Maine Bull., Vol.. XLV, No. 1. Univ. Maine, Orono. 197 p.

Hughes, E.L. 1976. A digest of silvicultural research at Green River, New Brunswick. Can. For. Serv., Maritimes For. Res. Cent., Fredericton, N.B., Info. Rep. M-X-66. 60 p.

Johnson, J.E. 1976. Growth and yield of evenaged spruce-fir stands in northern Maine as influenced by age, site index, and stand density. M.S. thesis, Sch. For. Resource, Univ. Maine, Orono. 142 p.

Ker, M.F. 1976. Metric yield tables for the major forest cover types of Newfoundland. Can. For. Serv., Newfoundland For. Res. Cent., St. John's, Newfoundland, Info. Rep. N-X-141. 79 p.

Lawrence, R.K.; Houseweart, M.W. 1981. Impact of the spruce budworm in the Maine spruce-fir region 1975-1979. Coop. For. Res. Unit, Res. Bull. 3. Sch. For. Resour., Univ. Maine, Orono. (Maine Agr. Exp. Sta. Misc. Rep. 250). 106 p.

Letourneau, L. 1966. A forest inventory by continuous forest control. For. Chron. 42:414-419.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56:213-221.

MacLean, D.A. 1985. Effects of spruce budworm outbreaks on forest growth and yield. Pages 148-175 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp. 16-20, Sept. 1984. Bangor, ME. Can. For. Serv., Ottawa, Ont.

MacLean, D.A.; Erdle, T.A. 1984. A method to determine effects of spruce budworm on stand yield and wood supply projections for New Brunswick. For. Chron. 60:167-173.

McLintock, T.F. 1947. Silvicultural practices for control of spruce budworm. J. Forestry 45:655-658.

McLintock, T.F. 1949. Mapping vulnerability of spruce-fir stands in the Northeast to spruce budworm attack. U.S. Dep. Agric., For. Serv. Northeastern For. Exp. Sta., Upper Darby, PA. Sta. Pap. No. 21. 20 p.

McLintock, T.F. 1954. Factors affecting wind damage in selectively cut stands of spruce and fir in Maine and northern New Hampshire. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Upper Darby, PA. Sta. Pap. No. 70. 17 p.

Meyer, W.H. 1929. Yields of second-growth spruce and fir in the Northeast. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. No. 142. 52 p.

Mott, D.G. 1976. The consequences of applying no control to epidemic spruce budworm. Pages 67-72 *in* Proc. of a symposium on the spruce budworm, 11-14, Nov. 1974, Alexandria, VA. U.S. Dep. Agric., For. Serv., Washington, D.C. Misc. Publ. No. 1327. 188 p.

Mott, D.G. 1980. Spruce budworm protection management in Maine. Maine Forest Review 13:26-33.

Mott, D.G.; Seymour, R.S.; Dimond, J.B. 1981. Integrated pest management for Maine forests. *In*: CANUSA Newsletter, Vol. 18.

New Brunswick Department Lands and Mines. 1958. New Brunswick forest inventory. New Brunswick Dep. Lands and Mines, Fredericton, N.B. 122 p.+ Appx.

Nova Scotia Department of Lands and Forests. 1980. Periodic annual increment — Province of Nova Scotia 1965-1980. Nova Scotia Dept. of Lands and Forests, Forest Resources Planning and Mensuration Division, Halifax, N.S. 162 p.

Page, G.; van Nostrand, R.S. 1973. Empirical yield tables for the major forest cover types of Newfoundland. Can. For. Serv., Newfoundland For. Res. Centre, St. John's, Newfoundland. Info. Rep. N-X-100. 84 p.

Safford, L.O. 1968. Ten-year average growth rates in the spruce-fir region of northern New England. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Upper Darby, PA. Res. Pap. NE-93. 20 p.

Schiltz, H.M. 1978. Growth and yield of evenaged spruce-fir stands in eastern Maine as influenced by age, site index, and stand density. M.S. thesis, Sch. For. Resource, Univ. Maine, Orono. 156 p.

Schiltz, H.M.; Reams, G.A.; Warner, W.S.; Corcoran, T.J.; Brann, T.B.; Solomon, D.S. 1983. Impact of the spruce budworm in Maine 1975-1980. Coll. For. Resour., Univ. Maine, Orono (Maine Agr. Exp. Sta. Misc. Rep. 290). 35 p.

Sewall, J.W. Co. 1983. Spruce-fir wood supply/demand analysis. Available from: Maine Dept. of Conservation, Augusta, ME. 94 p. + Appendices.

Seymour, R.S.; Mott, D.G.; Kleinschmidt, S.M.; Triandafillou, P.H.; Keane, R. 1985. GREEN WOODS Model — a forecasting tool for planning timber harvesting and protection of spruce-fir forests attacked by the spruce budworm. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Broomall, PA. Gen. Tech. Rep. NE-91. 38 p.

Solomon, D.S.; Frank, R.M. 1983. Growth response of managed uneven-aged northern conifer stands. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Orono, ME. Res. Rep. NE-517. 17 p.

Swaine, J.M.; Craighead, F.C. 1924. Studies on the spruce budworm (*Cacoecia fumiferana*). Part I. A general account of the outbreaks, injury, and associated insects. Canada Dept. Agric., Ottawa, Ont. Tech. Bull. 37 (new series), pp. 1-27.

Tothill, J.D. 1919. Passing of the balsam budworm in New Brunswick. Can. For. J. 15:306-307.

USDA Forest Service. 1981. Final programmatic environmental impact statement on the proposed cooperative five-year (1981-1985) spruce budworm management program for Maine. U.S. Dep. Agric., For. Serv. Northeastern Area, State and Private Forestry, Broomall, PA. 79 p. + Appendices.

Vincent, A.B. 1955. Development of a balsam fir and white spruce forest in northwestern New Brunswick. Canada Dept. of Northern Affairs and Nat. Resour., Forestry Branch, Ottawa, Ont. Tech. Note 6. 27 p.

Weed, D. 1977. Spruce budworm in Maine, 1910-1976 — infestations and control. Maine Dept. of Conservation, Augusta, ME. 100 p.

Westveld, M. 1941. Yield tables for cut-over spruce-fir stands in the Northeast. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., New Haven, CT., Occasional Pap. No. 12. 18 p.

Westveld, M. 1946. Forest management as a means of controlling the spruce budworm. J. Forestry 44:949-953.

Westveld, M. 1953a. Empirical yield tables for spruce-fir cut-over lands in the Northeast. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Sta. Upper Darby, PA. Res. Pap. No. 55. 57 p.

Westveld, M. 1953b. Ecology and silviculture of the spruce-fir forests of eastern North America. J. Forestry 51:422-430.

Yacavone, P.F. 1983. From stump thru mill — the great transition in the spruce-fir forest. Page 37-41 *in* T.J. Corcoran and D.R. Gill, eds. Recent advances in spruce-fir utilization technology, Proc. of a Symp., Univ. Maine, Orono, 17-19, Aug. 1983. 222 p.

Forecasting Growth and Yield of Budworm-Infested Forests. Part II: Western North America and Summary

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Forests infested with western spruce budworm (*Choristoneura occidentalis* Freeman) in western North America usually have lower yields than non-infested forests. Research conducted during the Canada/U.S. Spruce Budworms Program-West has increased our understanding of how budworm-caused damage affects tree growth, top-kill, mortality, and subsequent stand yields. Much of this research has been incorporated into the techniques used to forecast yields in affected forests. A single set of models has been constructed that combines what is known about forecasting budworm populations, the damage they cause, and the resulting forest yields in budworm-infested forests. Examples are presented to illustrate this set of models.

Dans l'ouest de l'Amérique du Nord, les forêts infestées par la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) ont un rendement inférieur à celui des forêts non infestées. Grâce à la recherche menée sous l'égide du programme CANUSA-Ouest sur les tordeuses des bourgeons, nous savons mieux comment les dommages causés par la tordeuse influent sur la croissance des arbres, le dépérissement des cimes, la mortalité et le rendement ultérieur des peuplements. La plus grande partie de l'acquis de cette recherche a servi aux techniques de prévision du rendement dans les forêts ravagées. Un ensemble de modèles construits combine l'information connue sur les prédictions des effectifs de la tordeuse, les dommages qu'elle cause et le rendement résultant des forêts. Des exemples servent d'illustration.

Introduction

Defoliation by the western spruce budworm (*Choristoneura occidentalis* Freeman) causes reduced diameter and height growth, destroys cones, kills the tops of trees, and sometimes kills whole trees. Top-killed trees often recover from the damage, but sometimes they are permanently deformed or defective. Yields from budworm-infested forests in western North America are usually lower than they would be in the absence of budworm.

Populations are seldom large enough to cause the widespread tree mortality typically experienced in eastern North America. This difference is the first of many that contrast the biological and technical aspects of yield-forecasting of eastern *vs.* western forests. Seymour (1985) has typified the conditions in the East and reviewed the methods used to predict the yields of affected forests. In this paper, the western methods are presented and eastern *vs.* western conditions and methods are contrasted.

Forest managers require yield estimates to choose from different silvicultural alternatives, schedule harvests, allocate lands among conflicting uses, and compute allowable cuts for management units. The management plan for a forest or sustained-yield management-unit documents the allowable cut and other decisions fundamental to forest management. Bible (1985) describes in detail the role of growth-and-yield models in the decision-making process. Here, the methods used to estimate yields are presented.

Before growth-and-yield simulation models were developed in the 1970s, managers had to depend on yield estimates based on local or regional yield tables and volume-over-time curves. Such estimates were commonly applied over large areas, and growth data on which they were based were updated infrequently. They generally do not take damage by pest organisms explicitly into account. When extensive damage to a forest occurs — such as in a budworm outbreak — surveys may be made to determine the immediate reduction in volume.

Evolution of Impact Estimates

B.C. Forest Service (1977)

A typical example of how budworm-caused damage has been taken into account in yield-forecasting is illustrated by a case in British Columbia (B.C. Forest Service 1977). During the late 1970s, an outbreak occurred in the Fraser River Drainage.

Because management plans for western Canada Public Sustained Yield Units are usually based on yield estimates that do not take budworm into account, methods were devised to modify the existing yield tables to account for two types of loss from budworm: reduction in growth rates of immature stands and degradation in quality.

Growth reduction was incorporated into the analysis by hypothesizing that 3, 6, or 12 years of growth would be lost during each outbreak cycle. These estimates correspond to optimistic, probable, and pessimistic forecasts.

The basic growth-reduction values and additional Canadian Forestry Service (CFS) estimates of losses indexed by outbreak duration were converted to increase in volume from spraying. This process took into account the number of hectares (acres) infested and the duration of the infestation.

From CFS field surveys, trees with forks, crooks, and other defects were estimated to have 15-percent less merchantable volume at harvest than sound trees, and 8 percent of the trees were estimated to be so damaged. These values (impact on quality) were translated into volume gains at harvest time.

The volume gains described above were used to modify volume-over-age curves applicable to each control unit. Although the report included citations for several of the factors, missing links were, of necessity, based on best estimates by knowledgeable scientists.

USDA Forest Service (1977)

The 1977 Environmental Impact Statement (USDA Forest Service 1977) for the Northern Region (northern U.S. Rocky Mountains), identified several studies linking budworm damage to reduction in radial growth, top-kill, and mortality. To estimate effects on yields, the approach was direct, as illustrated by the method used in the Beaverhead National Forest. Gross surveys were used to estimate that 8 percent of the timber base was infested, 60-percent net growth was lost per year of infestation, and 27.0 million board feet (63 720 m^3) annual growth was expected. The product of these numbers is 1.30 million board feet (3 068 m^3), which was used as the measure of volume lost because of budworm in the economic analysis.

USDA Forest Service (1983)

Volume curves may be modified directly to account for budworm damage. The 1983 Environmental Assessment (EA) for budworm (USDA Forest Service 1983) for eastern Oregon is an example of this technique. The assessment identifies growth loss, mortality, and top-kill as effects of defoliation. To take these effects into account, the Forest Service subtracted a gross loss of 4.3 years growth from volume at harvest to account for budworm. The methods were adapted from the 1977 British Columbia Forest Service report. Growth-loss data were taken from Gregg et al. (1979), who measured loss in eastern Washington. Volume curves were modified to reflect local conditions and then reduced by a flat rate to account for budworm. The analysis indicated that 587 560 hectares (1,451,890 acres) were infested in Oregon, and the infestation was causing a volume loss of 650,000 Mfbm (1.5 million m^3).

The eastern Washington survey further quantified and extended losses observed by Carolin and Coulter (1975), Williams (1966, 1967), and many others (see Johnson and Denton 1975). However, the analysts were still not satisfied with the resolution of their information. The EA states: "A budworm infestation is likely to have different impacts for the various stand conditions. Insufficient data existed for distinguishing these impacts. Therefore, an average was applied."

Summary of Approaches

These examples typify the evolution of impact estimation. Several other examples of these approaches to computing an effect on yields could be cited, but these analyses were precluded from direct application of empirically derived relations for several reasons:

- Relations needed to estimate loss are not available. The 1983 EA (USDA Forest Service 1983) for the eastern Oregon outbreak said that models that could be used to predict damage as a function of stand conditions were not available. The report indicates that had such models been available they would have been used; further, the analysts were convinced such a relation should exist.
- Some relations may be available, but unusable without additional linking relations which are themselves unavailable. For example, empirical yield tables may be the only form of yield forecast available to a forester. How can a top-kill model for an individual tree be applied to a stand-yield table?
- The technology necessary to apply knowledge may

exist, but not be used. Even if a detailed model existed, the time and skill required to run it across large land holdings and compile the results may not be available.

Quantifying Damage and Impacts

How can these three obstacles for not using better methods be overcome? Do we really have little data and understanding of budworms' effects on yields? Host responses to budworm damage have recently been reviewed and summarized by Van Sickle (in press). He recognized physiological effects on tree energy reserves, bud formation, foliage chemistry, stress, and predisposition to other pests. Physical changes included are effects on height, radial and volume growth, tree mortality, top-kill, root growth, and cone and seed production. Effects on stands include changes in stand structure and composition, reduced regeneration, and a summary of long-term effects on growth. Studies relevant to forecasting growth and yield are summarized below.

Thomson and Van Sickle (1980) describe an improved method of quantifying growth loss in Douglas-fir caused by pest activity. Methods were adapted from Duff and Nolan (1953) and Mott et al. (1957), which led to subsequent quantification of height, radial, and volume increments for the subject trees, which had been defoliated. Growth rates between outbreaks can be extrapolated to the periods when outbreaks occur. The difference between the no-outbreak extrapolation and the measured bole is taken as the damage-caused loss.

Alfaro et al. (1982) used Thomson and Van Sickle's methods to estimate radial-growth losses for four past outbreaks at Railroad Creek near Pemberton, B.C., Canada. The results of the analysis yielded a model that predicts proportional increment by year (PI_n):

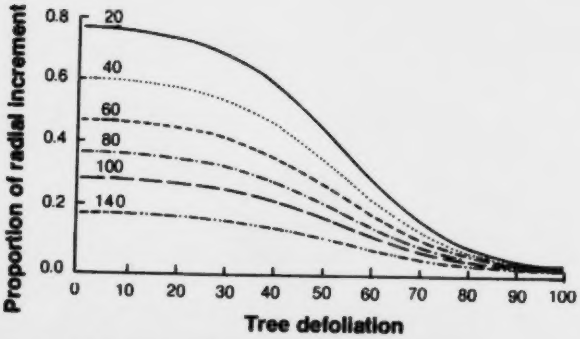

Figure 1. Proportion of radial increment as a function of defoliation history (DHIST = stand defoliation in year (n − 1) + year (m − 2)) and defoliation of the individual tree (from Alfaro et al. 1982).

$$PI = \frac{e^{-0.0126\,(DHIST)}}{1 + e^{-4.563\,+\,0.857\,(DEF)}},$$

where DHIST is the mean stand defoliation in year (n-1) + year (n-2); and DEF is the defoliation intensity for the subject tree in year n (Figure 1).

Alfaro et al. (1982) also reported two tree-mortality models. One predicts mortality as a function of diameter at breast height (dbh) and the other as a function of cumulative defoliation (CDEF), the sum of defoliation scores during the active feeding period.

Stage[1] suggested that these models could be combined into one function of dbh and defoliation:

$$Mort = e^{-21.83\,-\,2.07\,(DBH/\overline{DBH})\,+\,4.78\ 1n\ CDEF}$$

where Mort is percent mortality over the life of the outbreak (5 years of feeding followed by 5 years of recovery), DBH is the tree dbh, $\overline{DBH}$ is stand average dbh, and CDEF is cumulative defoliation, defined above (Figure 2).

Van Sickle et al. (1983) measured the effects of defoliation on height-growth loss and dieback. The average number of internodes lost on tress that showed dieback, over several outbreaks in British Columbia was 7.3, representing 15- to 20-percent loss of height relative to the estimated potential. In an earlier study, Collins and Van Sickle (1978) found that 35 percent of standing trees showed significant dieback.

The loss studies published by Thomson and Van Sickle (1980), Alfaro et al. (1982), and Van Sickle et al. (1983) are particularly important for the following reasons:

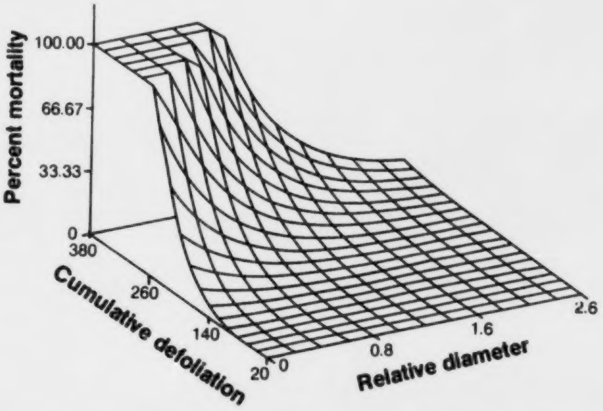

Figure 2. Percent mortality as a function of relative dbh (tree dbh divided by stand average dbh) and cumulative defoliation. Derived from two models published by Alfaro et al. (1982).

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[1] A.R. Stage, meeting in Stage's office, August 1983. Address: USDA Forest Service, Forest Science Laboratory, 1221 South Main, Moscow, ID 83843.

- The studies included direct measurements of defoliation on each sample tree for each year of the outbreak.
- Sophisticated computer techniques led to good estimates (Thomson and Van Sickle 1980) of what the potential growth would have been had budworm not been active.
- The analysis was not completed until after tree recovery was complete, affording a unique opportunity to measure long-term damage.

Williams (1967) related budworm damage to radial-growth and height loss of grand fir, Douglas-fir, and Engelmann spruce. He created four damage classes and demonstrated that radial increment was significantly lower in the higher defoliation classes. The greatest decline in increment occurred near the mid-crown and the least at the base of the bole. Height loss was expressed in terms of the number of years of height growth lost.

Carolin and Coulter (1975) compared budworm populations and damage between grand fir and Douglas-fir in Oregon and Washington. Grand fir was more heavily damaged than Douglas-fir, and damage was not related to different numbers of budworms. Their study of early tree damage indicated that the more heavily defoliated grand fir also experienced higher top-kill rates. None of the 18 dominant and 36 codominant Douglas-fir were top-killed after 4 years of defoliation that ranged from 10 to 98 percent. Of the 13 grand fir trees, top-kill occurred in those that were 97 percent to 99 percent defoliated and did not occur in those 94 percent defoliated or less.

Gregg et al. (1979) measured the effects of budworm-caused damage on understory stocking, top-kill and mortality, radial growth, and volume increment in north-central Washington. Budworm-caused damage was quantified by the number of years a plot was defoliated. An area was classified as defoliated in any given year if it was so indicated on aerial sketch maps; thus, the results cannot be extrapolated to forests that exhibit different defoliation patterns than those that typified this outbreak.

Results for the 5-year defoliation-class are as follows: regeneration stocking was reduced by 6.9 percent, and understory trees designated as potential crop trees increased in average dbh 9.16 percent. The increase was apparently the defoliation-induced release of nonhost species. Effects on the overstory include 1.3-percent Douglas-fir mortality and 9-percent top-kill. Grand fir was more severely damaged; 3 percent died and 12 percent were top-killed. Bousfield (1980) reported similar conditions in Idaho.

Two studies were conducted in the western United States that included detailed measurements of defoliation, as well as measurements of growth. One study by Ferguson and Stage[2,3] in Idaho and Carlson et al.[4] in Montana investigated the effects that western spruce budworm damage has on regeneration establishment and the development of small trees. Ferguson and Stage[2] noted a budworm-caused reduction in the probability of stocking and the number and size of trees on a stocked plot.

The other study was on the east side of the Washington Cascade Range.[5] Its objectives were to relate defoliation to height and diameter growth, top-kill, and mortality. A wide range of defoliation profiles and stand conditions were measured.

Recently, Scott and Nichols[6] reported results of the

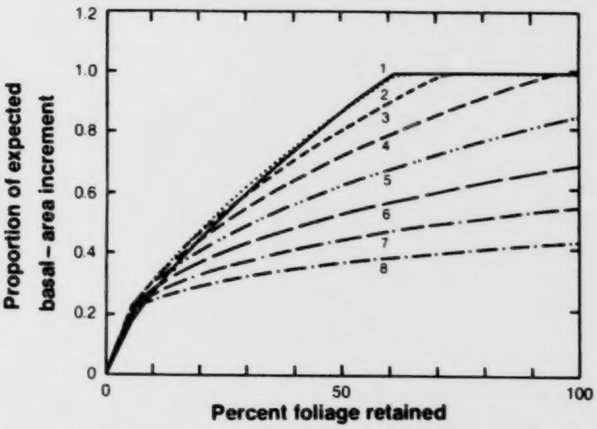

Figure 3. Proportional diameter growth as a function of percent foliage retained for eight values of DUREC. DUREC is the outbreak duration in years minus years of recovery. A similar function is used for proportion of expected height increment. Preliminary results from Scott and Nichols (see footnote 6).

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[2] Ferguson, D.E.; Stage, A.R. 1982. Impact of defoliation by spruce budworm on growth and development of young timber stands in Idaho. Progress report to CANUSA-West. On file at U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. 32 p.

[3] Ferguson, D.E.; Stage, A.R. 1982. The effects of spruce budworm on regeneration success in Idaho's forest ecosystems. Progress report to CANUSA-West. On file at U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. 32 p.

[4] Carlson, C.E.; Theroux, L.J.; McCaughey, W.W. 1982. The influence of silvicultural practices on the susceptibility and vulnerability of northern Rocky Mountain Forests to the western spruce budworm. Progress report to CANUSA-West. On file at U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. 37 p.

[5] Scott, D.R.M.; Crimp, P.M.; Johnsey, R.L. 1980. Growth impacts on host trees due to western spruce budworm defoliation on the east slope of the Washington Cascades. Final report to CANUSA-West. On file at U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 111 p.

[6] Scott, D.R.M.; Nichols, T. 1983. Growth impacts on host trees due to western spruce budworm defoliation on the east slope of the Washington Cascades. Final report to CANUSA-West. On file at U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 71 p.

initial analysis. The amount of defoliation recorded did not result in top-killing or mortality. Height and diameter increment were reduced by budworm, however, and were related to the duration of the outbreak — minus the recovery period in years and the proportion of retained biomass (Figure 3).

To compute the proportion of expected growth, the observed growth is divided by an estimate of potential growth. Scott and Nichols[6] used the height and diameter subcomponents of the Prognosis Model (Stage 1973; Wykoff et al. 1982) to predict potential growth for use in their analysis. The self-calibration feature of the Prognosis Model allowed partial correction of the effects that changing weather conditions had on observed growth. Nichols[7] has since found, however, that a more accurate method of predicting expected growth is to use weather records and non-host growth rates. The preliminary results obtained using this technique are an improvement over the relations displayed in Figure 3, and will replace them when available.

Applying Research Results

Results from various studies during the past several years can be applied to the problem of estimating future yields.

The Prognosis Model

Development

In the late 1960s, Stage (1973) developed the Prognosis Model, designed to simulate the development of the mixed-species, even- and uneven-aged stands commonly found in the northern Rocky Mountains. Usual inputs for the Prognosis Model are a list of sample trees and stand characteristics obtained from standard (United States) stand inventories (Stage and Alley 1972). The model is a distance-independent, individual-tree model that predicts how a current inventory of trees will grow under various, user-specified thinning regimes and in natural conditions.

Since its introduction, the model has grown and evolved. Regional variants have been or are being calibrated for northern California, Montana, eastern and southern Oregon, Utah, Alaska, British Columbia, and Idaho. Specifics on submodel structure and development are given in Stage (1973, 1975), Hamilton and Edwards (1976), Monserud (1980), and Wykoff (1983). A user's guide has been prepared by Wykoff et al. (1982).

The first pest-impact study specifically designed to be linked with the Prognosis Model was for the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Crookston et al. 1978; Crookston and Stark 1985). A population dynamics simulation program for mountain pine beetles was coupled to the Prognosis Model for stand development. Together, they provided a unified program that could be used by forest managers and researchers to estimate the effects of mountain pine beetle on stand growth and explore management alternatives designed to reduce losses.

Almost concurrently, an outbreak model was developed for the Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough), which simulates the course of an outbreak and the impact of forest stands (Colbert et al. 1979). This also was linked to the Prognosis Model (Colbert and Campbell 1978; Monserud 1978; Monserud and Crookston 1982; Stage 1978a-e).[8]

The obvious utility and apparent success of these combined models influenced the research planning of the western component of CANUSA. From the outset, an objective was to develop comparable models for the western spruce budworm linked to the Prognosis Model.

Using the Prognosis Model

The user enters a sample-based inventory of trees from one stand. Data entered for each sample tree generally includes dbh, species, crown ratio, and height. A subsample of diameter increments on large trees and height increment on small trees is also entered. Other tree variables include tree-history code, tree-value class, and short-run prescription code. Stand variables include forest code, habitat-type code, aspect, slope, and elevation.

The model starts (Figure 4) by summarizing the current inventory. Past growth increments are compared to the model average, and the difference is used to adjust the model constants to reflect the unique site and tree qualities of each stand. The results of this self-calibration and the current stand attributes are displayed. Then, thinning options are simulated and post-thinning densities are computed. Periodic diameter and height increment are computed for healthy tree growth. In the absence of the Budworm Model, normal periodic mortality rates are estimated. The period length is generally set at 10 years, but may be specified by the user. Increments are added to beginning-period tree dimensions, and individual-tree mortality rates are subtracted from the tree sampling weights. Individual-tree volume is computed using diameter, height, point of top-kill, species, and user-specified form and defect adjustments. Stand statistics are computed from individual-tree values. The conditions at the end of the growth period are displayed. The crown ratios are changed to reflect either an increase or decrease in crown lengths. Then the model cycle is repeated.

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[7] Nichols, T. 1984. Western spruce budworm impact model calibration. Final report to CANUSA-West. On file at U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 74 p.

[8] Monserud, R.A. 1978. Implementation of prognosis model for forest stand development for combined assessment of silvicultural and DFTM control activities. Final report to the DFTM Program. On file at U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Moscow, ID. 90 p.

The Prognosis Model is used in a variety of ways by many people. It is used by forest planners to construct yield tables applicable to classes of stands and management regimes. These tables are used when constructing a management plan for a forest. The model is used by silviculturists to test prescriptions designed for individual stands or cutting units. Although the model was designed to project the growth of a stand of trees, it is often used to project a class of plots from disparate locations. Then, care is given to the classification to ensure that consistent site and habitat characteristics are found at each sample location.

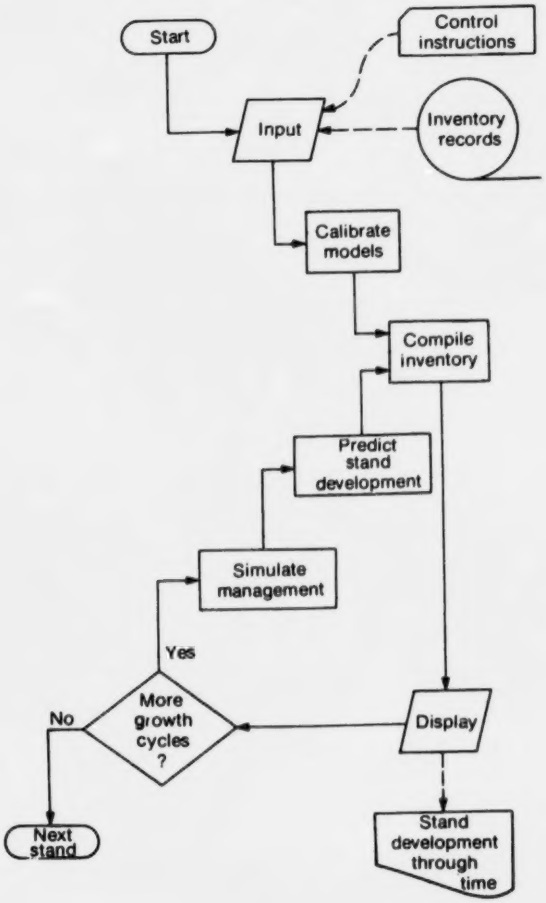

Figure 4. Conceptual, low-resolution flow diagram of the Prognosis Model (from Wykoff et al. 1982).

In addition, adjusting the model can extend its geographic range. One method is to modify the intercepts of the increment models according to average calibration terms. Wykoff et al. (1982) discuss these techniques in the user's guides. Using these techniques is safer when the differences between yield forecasts are used to make decisions rather than using the absolute yields.

Example 1: No Budworm

The Prognosis Model is being used by the forest silviculturist on the Malheur National Forest, central Oregon, to prepare yield tables for the forest plan. One of the mixed-conifer timber classes from the Malheur is used as an example in this paper. Together, the inventory plots represent a composite of land at about 5,500 feet elevation; forest age is about 80 years, and species composition is grand fir, Douglas-fir, ponderosa pine, and a very small component of lodgepole pine and western larch. Current inventory is 1,058 trees per acre, 3,000 cubic feet per acre, and 15,000 board feet per acre.

The management regime for this area includes an overstory removal to a 14-inch diameter limit and a precommercial thinning from below during the first decade to 360 trees per acre. After that, density control is maintained at 80 to 121 square feet of basal area. Thinnings are scheduled whenever density is about 121 square feet, given that at least 3,000 board feet of volume can be removed without dropping below 80 square feet of basal area. The diameter distribution of cut trees includes the overly large, perhaps mature trees and sufficient additional suppressed and codominant trees to achieve the target density.

Figure 5 contains a pair of volume-over-time curves created by running the Prognosis Model for this mixed-conifer example. Line A is a plot of the standing volume; removals are shown by the sharp declines in volume. Line B is total production; the removals are summed as they occur, and the sum is added to standing volume. Total production is useful when comparing yield forecasts that contain various numbers and intensities of thinnings or other changes. The usefulness of this statistic will become more apparent in the following examples.

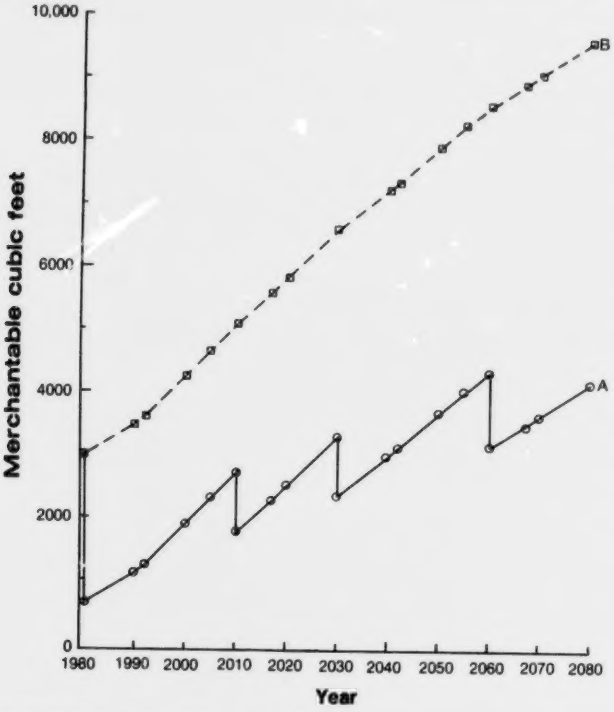

Figure 5. **Standing merchantable volume per acre (line A) and total production merchantable volume per acre (line B) for a mixed-conifer timber class from the Malheur National Forest. Total production is computed by adding the sum of removals to date to the standing volume. The results of budworm-caused damage are not shown in this figure.**

Four thinnings are simulated. The first is in 1980, the second in 2010, the third in 2030, and the fourth in 2060. Actual management of this timber would probably result in final harvest occurring near 2060 or 2070. Figure 6 is a plot of mean annual increment (line A) and periodic annual increment (line B). Variability in periodic annual increment is normal in nature; the variability displayed in Figure 6 results from the stochastic component of the Prognosis Model. A quadratic regression line (form is $y = b_0 + b_1X + b_2X^2$) is displayed to smooth out the random variation in periodic annual increment. Culmination of mean annual increment occurs near year 2060, thus further supporting the idea that final harvest would be scheduled about then.

Care should be taken when interpreting mean annual increment in Figure 6 and other similar figures. In this paper, mean annual increment is the total merchantable production divided by stand age. The ages of trees represented here are variable; under a strict definition, this stand might not be considered even-aged.

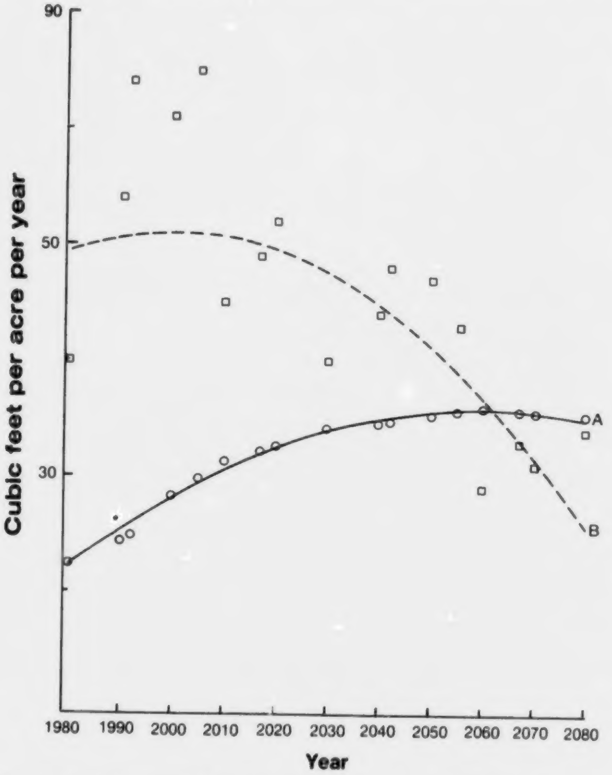

Figure 6. **Mean annual increment (line A, total production of cubic foot volume per acre divided by current age) and periodic annual increment (line B, accretion in cubic feet per acre per year minus mortality in cubic feet per acre per year) for the same projection illustrated in Figure 5.**

Example 2: Modifying Prognosis-Model Predictions[9]
One method of estimating yields for budworm-infested forests is to modify the Prognosis Model predictions such that normal growth increments are reduced and mortality rates are increased to reflect damage. Alternatively, growth rates could be increased to reflect protection; this would only be appropriate if the normal increments were produced with implicit amounts of budworm damage. To change the predictions, a model user enters growth or mortality multipliers or both; different multipliers can be entered for each species and Prognosis Model cycle. Height and diameter growth can be controlled separately on regeneration and large trees. Mortality multipliers can apply to any user-defined diameter classes.

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[9] Note that all of the methods of using the Prognosis Model to represent budworm damage, including this crude one, were developed with support of the CANUSA-West Program.

Multipliers were used in the Prognosis Model to provide yield tables for the Boise and Payette National Forests 1979 Environmental Statement (USDA Forest Service 1979). Economic analysis required detailed yield tables for each spray block, timber type, and management alternative. Appropriate growth-rate multipliers were computed from Forest Pest Management (FPM) Survey data. Rates of budworm-caused tree mortality were found to be 3.71 times higher than normal for grand fir; other species exhibited no such increase. Radial growth of Douglas-fir was 82 percent of normal, and grand fir grew 69 percent of normal.[10] No data existed for subalpine fir and spruce. The Douglas-fir growth reductions were used for spruce and those of grand fir for subalpine fir.

Although data were available on rates of top-kill, they were not included in the analysis because the necessary computer programming could not be done in time.

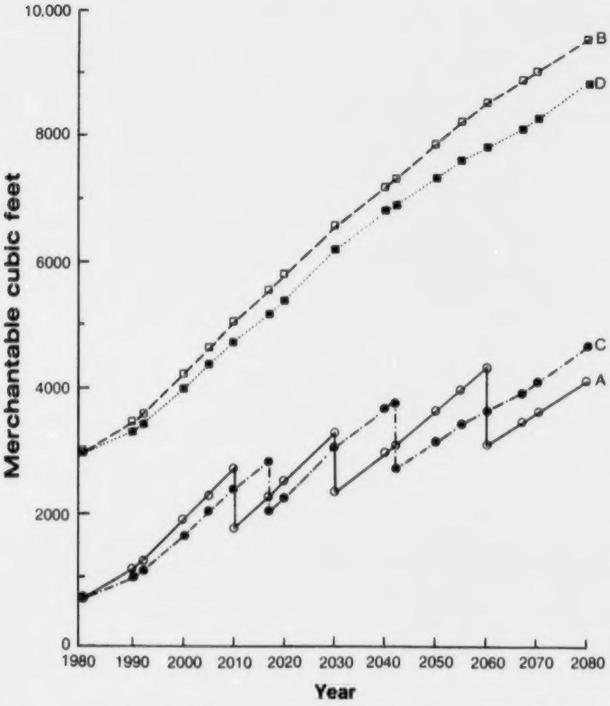

Figure 7. **Lines A and B correspond exactly to lines A and B in Figure 5. Line C is the stand volume derived when budworm damage occurs as explained in example 2 (growth and mortality multipliers are used) and can be compared to line A. Line D can be compared to line B to show the effects of budworm damage on total production.**

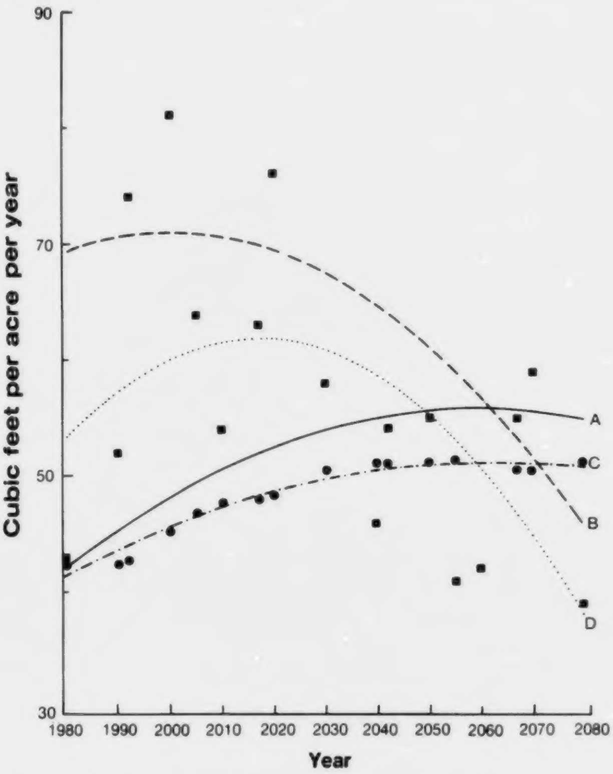

Figure 8. **Lines A and B are exactly the same as in Figure 6 except that the data points are not shown. Lines C and D may be compared to A and B, respectively; they show the effects of budworm damage on mean annual increment and periodic annual increment as discussed in example 2 (growth and mortality multipliers are used). Line D is fit to the widely scattered solid square data points.**

Budworm outbreaks were assumed to recur every 13 years and last for 12 years. Thus, growth reductions were applied for the 12-year outbreak period and the stands allowed to grow normally for 13 years. The effect of these multipliers are displayed in Figures 7 and 8, which are yield curves and plots of periodic annual increment and mean annual increment for the same example referred to in Figures 5 and 6. Although this example is from the Malheur National Forest rather than the Boise or Payette National Forests, it serves to illustrate the effects on stand growth that these growth and mortality multipliers can have when used to modify predicted tree growth.

The effect of the budworm, as represented using the multipliers, on standing volumes (line C, Figure 7) is very small — probably insignificantly different from growth without budworm (line A). The amount of volume removed at each thinning, the number of commercial thinnings, and the schedule of thinnings are different.

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[10] These data are taken from a letter sent to D. Smith, Boise Cascade Corporation, P.O. Box 50, Boise, Idaho 83738, on January 16, 1978, by the author, who has a copy of the letter on file.

Both runs were made with the same thinning rules, as described above. The resulting reduction in total production is illustrated by comparing lines B and D. Budworm clearly reduced the total production of this mixed-conifer timber class — at least, when these multipliers are used to represent budworm-caused damage.

Periodic annual increment and mean annual increment with and without budworm can be compared (Figure 8). The rather wild variation in periodic annual increment is caused by the periodic effects of budworm. The net effect of slowing growth and increasing mortality is to reduce periodic annual increment temporarily; then, recovery returns growth to normal or above normal conditions. Even so, note that the quadratic regression line with budworm (line D) bisects the mean annual increment (line C) a little sooner than periodic annual increment (line B) bisects mean annual increment (line A) without budworm. Therefore, the model predicts earlier culmination of the mean annual increment in this budworm-infested timber type than without budworm.

As we have seen, budworm-caused damage can be crudely represented using the Prognosis Model directly, but it falls short of representing the known types of tree damage and the amounts of that damage. The model is an improvement over the previous simple methods of modifying yield tables because field measurements of individual-tree mortality and growth rates can be used directly in the calculations, and the effect of budworm damage in mixed-species and mixed-age stands is represented without aggregating average effects and applying the average to all stands.

The Combined Prognosis-Budworm Model

The western component of the CANUSA program has focused its attention on developing the combined Prognosis-Budworm Model. This model contains enough detail to represent a great deal of knowledge about tree growth and budworm dynamics. The combined model has recently been described by Sheehan et al. (in press); also see Colbert et al. (1983).

Recall that the damage models described above use some measure of defoliation as one of the independent variables. An improvement over the use of growth- and mortality-rate multipliers would be to let users enter annual defoliation rates, by host species and tree-size classes. The model could then translate this defoliation into growth reduction, mortality, and top-kill using the models described above.

Although tree defoliation is measured in the field in a variety of ways, the combined model reports just two measures of defoliation. Total-tree cumulative defoliation is taken to mean the percent foliage missing from all age classes; current defoliation is the percentage missing from the new foliage only and is carried in the model by foliage cohort. Because different damage models each expect different measures of defoliation, a portion of computer code was constructed that computes all of the measures of defoliation using current defoliation as a driving variable. The same computer code is used by the Budworm Model (described below) to translate between defoliation measures when it is used to estimate defoliation.

Foliage Dynamics

The foliage dynamics component of the Prognosis-Budworm Model estimates the amount of foliage biomass on each host tree using equations developed by Moeur (1981). These estimates are then divided into foliage age-classes and assigned to crown thirds. The foliage model changes the foliage profile in response to defoliation and computes annual potential foliage to use as a denominator to calculate percent defoliation (Sheehan et al., in press). The concepts reviewed by Van Sickle (in press) and used by Thomson (1979) on loss of energy reserves and creation of adventitious buds are used in this component.

Damage Models

The Damage Model component translates defoliation into reduction in diameter and height growth, using Scott and Nichols' models (Figure 3).[11] Mortality is predicted by the greater of the base Prognosis Model rates, and Alfaro's models as modified (Figure 2; this represents a large extrapolation of Alfaro's models). Three types of top damage can be simulated. Total loss of height growth for 1 year is accounted for in the height-growth-reduction component (Figure 3b). Top-kill with and without permanent defect is predicted such that the rates measured by Gregg et al. (1979) are simulated. The effect of top-killing on volume is represented using methods developed by Monserud (1980). Another option allows the user to enter the probability of top-kill and the proportion of crown killed during an outbreak into the Prognosis Model cycle.

Example 3: Using the Foliage and Damage Models

The damage component of the Prognosis/Budworm Model was used by the Malheur National Forest in north-central Oregon in 1983 to estimate the effects budworm-caused damage have on yields (USDA Forest Service 1984). The Budworm Model was not yet completed, so the analysis was made without it. Forest Pest Management entomologists entered defoliation-survey data into the damage model to characterize the defoliation profile expected for each outbreak. One outbreak was simulated every 25 years; the outbreaks last for about 10 years.

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[11] Scott and Nichols' models are applied assuming that all sample trees in a tree-size class are equally defoliated. This assumption is not required; new damage models are being implemented that account for variation in defoliation between trees in each class.

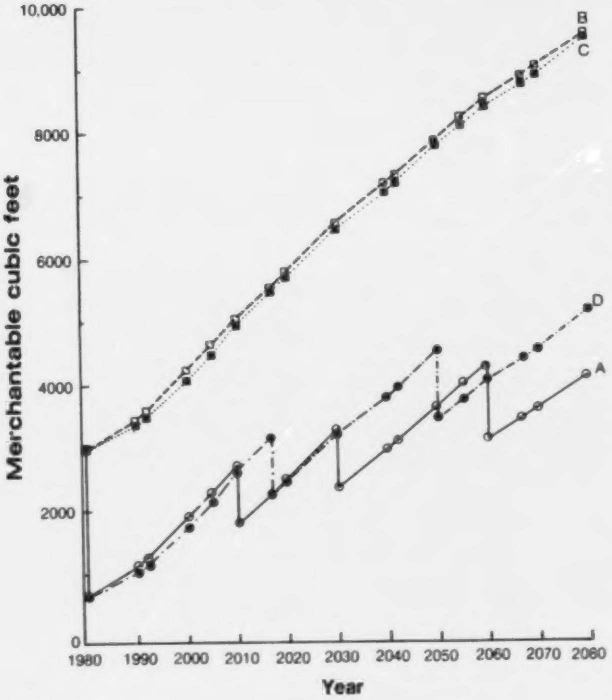

Figure 9. **Lines A and B are exactly the same as in Figure 5. Lines C and D are standing volume and total production under the damage regime described in example 3 (defoliation estimates are used).**

Comparing Figures 7 and 9 illustrates that the effect budworm has on total production is less using the newer models. This difference can be attributed to the following.

- The defoliation rates actually measured in the Malheur National Forest are lower than those on the Boise and Payette National Forests. The resulting damage would be appropriately lower.
- The damage models simply predict smaller amounts of growth loss for the same amount of defoliation than implied in the multipliers used in the 1979 Environmental Assessment.

A shift in the thinning schedule resulted in the loss of one commercial thinning (Figure 9). Reduced total production is shown for this method of yield estimation for the example timber type. Figure 10 illustrates the relative projections of mean annual increment and periodic annual increment using this method to represent budworm-caused damage as compared with example 1 without budworm.

Example 4: A Silvicultural Option

This sample timber type contains about 200 ponderosa pine trees of various sizes per acre. The thinnings simulated in examples 1 to 3 do not favor any particular species over another. What would happen if we saved as much ponderosa pine as possible, while otherwise meeting the target residual-stand density and the minimum harvest criteria outlined above?

Figure 11 illustrates the resulting change in total production (lines B and D) and standing volume (lines A and C) assuming no budworm. At year 2040, the total production of the "save PP" projection (line D) starts to depart from the "no-preference" (line B) projections. This happened because many of the ponderosa pine were growing in the understory for the first 60 years. The second commercial thinning in year 2030 released what had become a pole-sized ponderosa pine understory. The resulting total production at year 2080 for the "save PP" run (line D) is about 400 cubic feet per acre greater than the "no-preference" run.

Lines A and C show that the commercial yields in the thinnings scheduled for 2040 and 2060 in the "no-preference" run (line A) were slightly higher than the thinnings done in the "save PP" run (line C). Figure 12 demonstrates that the culmination of mean annual

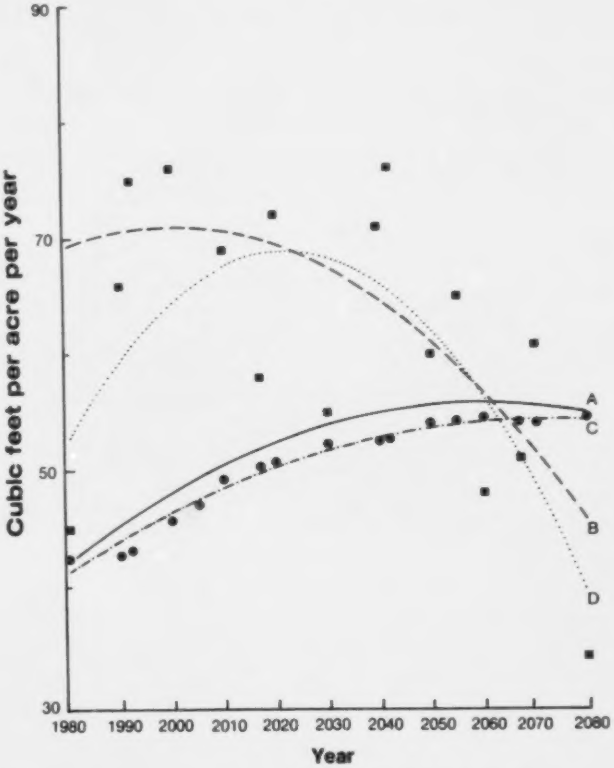

Figure 10. **Compare line A to line C to see the effects of budworm on mean annual increment and compare line B to D to see the effect on periodic annual increment. Line D is fit to the widely scattered solid square data points. The runs presented here are also presented in Figure 9; lines A and B are identical in Figure 6 except that the data points are not shown.**

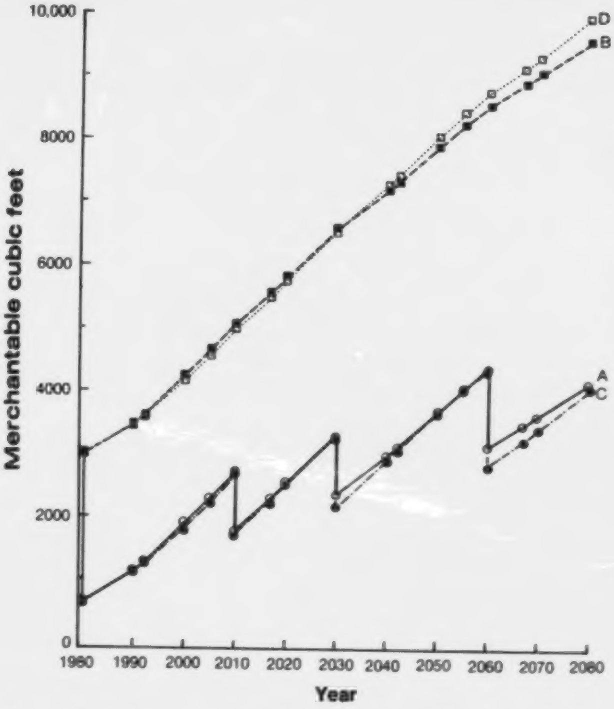

Figure 11. No budworm damage is represented; see example 4. Compare line A (identical to Figure 5) to line C to see the effect that saving ponderosa pine has on projected standing volume. Line B (identical in Figure 5) can be compared to line D to see the effect on total production. When budworm damage is added to the example displayed here, the graph is almost identical. Total production was slightly higher with budworm damage, however.

increment will occur about 15 years later in the "save PP" run as compared to the "no-preference" run. What does our new silvicultural plan do to budworm-caused losses in volume? A simulation run using the "save PP" management options and the budworm options used in example 3 demonstrated that more total production was achieved with budworm than without. No figures are presented to illustrate this case. The statistics are nearly identical to those displayed in Figures 11 and 12, except that the total production was 10,119 cubic feet per acre with budworm and 9,948 cubic feet per acre without (line D, figure 10).

Placing Examples Into Perspective

The major point in using this mixed-conifer example is not to show that budworm is not a problem in western North America. Another example, with realistic defoliation rates in a typical all-host stand, could have been used to demonstrate clearly that the budworm is a problem.

These examples should not be viewed as clear evidence that foresters always have silvicultural options to mitigate budworm-caused losses. Nonhost trees could be unresponsive to thinning, susceptible to a different pest later in the life of the stand, or both. For example, lodgepole pine would probably be killed by mountain pine beetle had it been selected for management.

Further, this mixed-conifer class may not have homogeneous species composition. The 200 ponderosa pine per acre may not be evenly distributed in the sample plots that form this timber class. If that is true, the results demonstrated in Figures 11 and 12 are invalid. If the species composition is similar throughout the sample area, the results are probably valid. The model user bears the responsibility for formulating the input data and understanding the implications of the results.

The major points that the examples illustrate are:

- The outputs of the Prognosis-Budworm Model are yield tables. The input is a current inventory of stand conditions and as much knowledge as possible

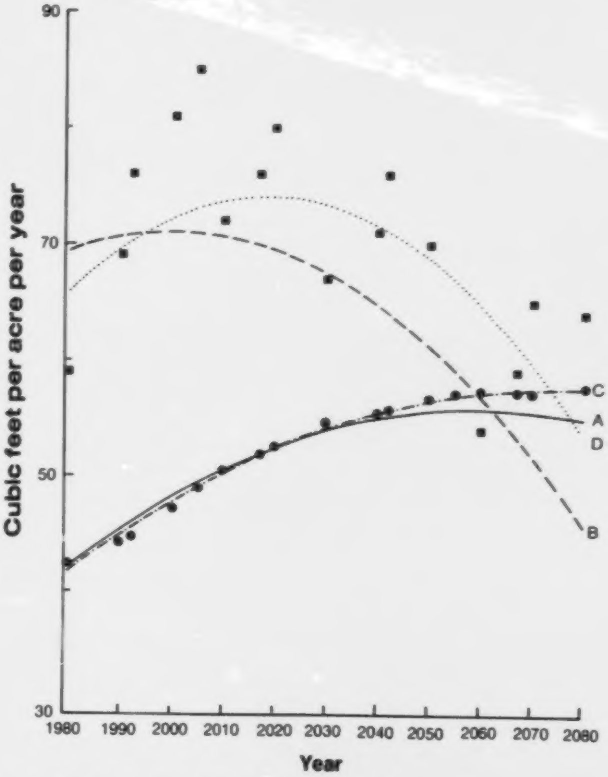

Figure 12. Lines C and D show that culmination of mean annual increment occurs 15 years later and at a greater growth rate than indicated by lines A and B (identical to Figure 6 except data points are not shown). This figure displays the "save PP" option described in example 4 and illustrated in Figure 11.

concerning the expected life and management of the stand.

- Many decisions are made by comparing management alternatives. Therefore, the models need to respond to the alternatives that are being contemplated. Further, the relative difference in response is more important than the absolute values.
- Preliminary research and development results, such as those used in all the examples presented in this paper, are useful in forest management decision-making.
- Foresters, entomologists, and other practitioners of forestry need to adapt their analyses to new research and developments.
- Because none of the examples of yield forecasting in budworm-infested forests presented so far have exercised the Budworm Model, a great deal of research and development that can give us more confidence in our ability to foretell the future is just becoming available.

Budworm Model

Realistic yield forecasting in budworm-infested forests requires knowledge of when defoliation will occur, how severe it will be, how it may be influenced by management actions, and how it varies with tree size and species composition.

The Budworm Model is designed to be sensitive to changing stand conditions through natural or imposed (management actions) processes. It can be used to simulate insect-control options, which include augmenting predators and applying chemicals, virus, or bacteria. It is a detailed, mechanistic, population-dynamics model that simulates budworm development throughout its life cycle. See Sheehan et al. (in press) for a complete overview of the Budworm Model.

During each year of a budworm outbreak, foliage values are updated by the foliage-dynamics component, and the Budworm Model is called. The Budworm Model predicts the reduction in foliage at the end of each year of defoliation and returns this information to the Prognosis Model for use in the damage component.

Predicting When Outbreaks Will Occur

Two options are used to start an outbreak — one allows the user to specify the year an outbreak will occur. The Prognosis Model automatically starts an outbreak during that year. The second option uses historical data on frequency of outbreaks to generate the probability of outbreak occurrence (Kemp 1983). At the start of a Prognosis Model cycle, the model can use the probability function to predict whether an outbreak will occur in the region during that cycle. If the species composition of the subject stand includes a primary host (Johnson and Denton 1975), it is considered infested if the surrounding area is infested.[12]

Weather Model

Degree-days are computed from daily maximum and minimum temperatures simulated using a weather generator adapted from Bruhn (1980) and Bruhn et al. (1979) by Kemp (in Sheehan et al. in press).

Two options are provided for predicting daily maximum and minimum temperatures. One uses weather records for a particular location to create site-specific climatic parameters. The Weather Model uses these to simulate daily weather. The second allows users to specify actual daily weather.

When daily weather is simulated, daily temperatures are a function of month, rainfall the previous day, and a random variable described by a normal probability distribution.

Adult Dispersal

When budworms emerge as adults, the model assumes that a percentage lay some eggs and then disperse. Some adults leave the stand they developed in; others do not. The Adult Dispersal Model simulates this activity and assigns a post-dispersal egg population to each stand in a run.

One option allows the user to select a net dispersal rate which serves to account for a gross loss (or gain) of eggs from the population. Another simulates dispersal as a function of the distances between stands, maximum dispersal range, and host foliage in each stand.

Parallel-Processing Extension (PPE)

The Parallel-Processing Extension is an extension to the Prognosis Model that allows up to 200 stands to be processed together, in a parallel fashion. It requires that each stand in a run be entered sequentially, projecting all stands one increment before subsequent increments are computed. This mode of processing differs from the regular Prognosis Model, which projects one stand for several increments before another stand is entered. The PPE has many uses[13]; it is used by the Budworm Model because it can maintain the status of several stands at once, allowing the simulation of adult dispersal to be included in long-term projections that include several stands.

Future work on the Budworm Model and its linkages to the Prognosis Model will result in a combined model that contains most of our current understanding of the budworm and its hosts. When these combined models are available, they will be useful in making yield forecasts in budworm-infested forests.

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[12] Ulliman, J.J.; Kessler, B. 1983. Validation of a spruce budworm aerial photo/risk model. Final report to CANUSA-West. On file at U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 87 p.

[13] Crookston, N.L. In preparation. User's guide to the Parallel Processing Extension of the Prognosis Model. Gen. Tech. Rep. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. (Review draft dated 30 November 1983 on file with Project Leader, RWU-1302, For. Sci. Lab., Moscow, ID 83843.)

Summary of Western Work

Yield-forecasting methods in the West have evolved; as new data and analyses are completed, the results have been used to improve yield-forecasting technology. The primary approach has been to add component models and programs to the Prognosis Model. Thus, this distance-independent individual-tree stand model has provided a sufficiently detailed description of the forest to model budworm-caused damage and its effect on yields. Two successively detailed methods to use this model have been demonstrated here: the use of growth and mortality multipliers and entering defoliation estimates. A third method, using the Budworm Model to estimate defoliation so that the damage models can modify growth, has been described.

The effects of budworm defoliation on stand yields in the West is small compared to preconceived ideas. The variance is high: stands with a large component of nonhost can actually benefit from defoliation, and heavily infested immature stands of pure host can experience large reductions in volume. The combined Prognosis-Budworm Model predicts these effects. In addition, the model is sensitive to most management regimes anticipated for use in the West. Thus, the model can be used to compute the differences in yields expected under various management regimes.

The combined model and its components were developed largely from CANUSA-sponsored research. In the relatively short life of the program, however, many questions could not be resolved — precise simulations of impact caused by budworm defoliation require long-term measurements of tree and stand growth during and after outbreaks. The ultimate effect of defoliation is not known until the trees have either had time to recover or to die.

Research and Development Needs in the West

The following work needs to be done to complete the job of producing good models:

- A function needs to be developed that predicts the probability that a forest or stand will be infested during a given interval, say 5 years, with a specific, somehow defined population of budworm. Given the probability of an outbreak's occurring, the expected yields can be computed. Without this function, model users are forced to provide educated guesses as to where and when outbreaks will occur. Progress toward meeting this task has been attained by Heller et al.,[14] Kemp (1983), and Ulliman and Kessler (see footnote 12). Additional work is needed.
- Ferguson[15] has not yet completed his work on regeneration. A model that represents "normal" establishment (i.e., without budworm) has been developed (Stage and Ferguson 1982) and linked to the Prognosis Model (Ferguson and Crookston 1984). Once budworm effects are quantified, they will be added to this model so that the benefits of mitigating damage can be computed. Budworm populations have continued in the study areas; reduced height growth, tree mortality, and damage are occurring there; and Ferguson does not have funding to continue the work until the budworm-damaged trees have recovered. This opportunity to understand the effect of the budworm on regeneration development should not be lost.
- The computer programming necessary to complete the linkages of the Budworm Model to the Parallel-Processing Extension is not complete. This work is needed so that long-term projections of several stands can be based on reasonable assumptions about adult dispersal, and also because the Parallel-Processing Extension promises to help automate the task of running the models over large, diverse working circles.

Eastern and Western Work

The eastern and western approaches to forest management and yield forecasting differ significantly. I will emphasize points that can lead to furthering research and improving forest-management practices for both regions.

At the root of the differences is that the demand for yield-forecasting has been present in the inland Northwest longer than it has been in the East. Emphasis on yield scheduling using volume control and on managing stands with much diversity in species and age placed an early demand on forecasting tools that could discriminate among many silvicultural options. In the East, management emphasized area control to regulate the flow of yield. As long as growth and harvest volume were about even, regulation was thought to be accomplished (Stage see footnote 1), and yield forecasts were not needed.

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[14] Heller, R.C.; Ulliman, J.J.; Anderson, H.N. 1981. Use of photo interpretation and remote sensing techniques to establish hazard rating criteria for spruce budworm susceptible stands. Final report to CANUSA-West. On file at Coll. For. Wildl. and Range Sci., Univ. Idaho, Moscow. 48 p.

[15] D. Ferguson, meeting in Ferguson's office, June 1984. Address: USDA Forest Service, Forest Science Laboratory, 1221 South Main, Moscow, ID 83843.

Centralized ownership and management of western forests lent itself to the application of volume control over wide areas. Interest in yield forecasts was enhanced as harvests approached the allowable cut. When harvests are well below the allowable cut, grossly conservative estimates of allowable cut are sufficient. As demand increases, the need for reliable yield forecasts increases because those forecasts are the justification needed to use less conservative, higher allowable cuts. This increase in demand is now occurring in British Columbia, resulting in a keen interest in the development of new forecasting tools. In fact, a version of the Prognosis Model is being constructed for part of British Columbia.

By contrast, the forest-management approach in the East has been to build models applicable to state-wide or province-wide decisions. The results have been models like WOSFOP and the Green Woods Model (Seymour, 1985; Seymour et al. 1985). Output from these models and others has been used to support policy decisions by corporations, states, and provinces. At that scale, similar modeling approaches are often used in the West.

Emphasis has been placed on representing a stand and its context in the forest in the CANUSA-West modeling work. The legacy of the Prognosis Model has been to represent stands because they are biologically meaningful units of land and are managed as units. Sample-based linkages to making forestwide inferences have been worked out by Stage and Alley (1972), and refined by the National Forest System professionals who have applied the technique. Direct linkages have been made between identified land units and the accompanying management alternatives, which can be traced through the yield-forecasting step. The decision-maker can then contrast alternatives in light of any additional knowledge of the stands under consideration. The variation between stands is thus retained, rather than lost in a class average. This is true for all steps in the management process. At least it can be true; sometimes the linkage between a management plan and the land it applies to becomes lost. Timber-type classes may be used in place of sampled stands, as in the examples presented in this paper. The possible consequences of not representing variance in species composition have been described.

The large difference in modeling approaches between the East and West cannot, in my opinion, be traced to fundamentally different biological systems. The forests in the inland Northwest and the Northeastern United States are diverse in age and species composition. Recent information from forest inventories indicates that perhaps as much as half of the forest resource in the Northeastern United States could not be classified as even-aged (J. Barnard[16]). Spruce-fir forests are intermixed with hardwood forests. I believe the general approach taken in the West is applicable in the East because it was designed to handle the high variance typically found in forests.

The modeling approaches in the East typically require stand-growth functions or yield tables as input. The growth and mortality rates implied by those tables are then adjusted to account for budworm damage. Research on quantifying growth and mortality at the stand level is included in these models.

This approach is not used in the West. Growth and mortality of individual sample trees are predicted by the Prognosis Model, and these predictions are modified to account for budworm. Then, the volume of the stand is computed by summing the volume of the individual trees. Research on understanding and quantifying growth and mortality of individual trees in the presence and absence of budworm is included in these models.

Conclusions

Yield-forecasting models have been presented by Seymour and in this paper that have provided information on managing budworm-infested forests. Although they are only approximate in some respects, they are useful.

A large body of research results on budworm dynamics and forest growth is available. Much of this knowledge is relevant to yield forecasts; however, only when it is systematically organized can it be applied readily. Models need to be formulated so that they provide the needed outputs from reasonable data inputs. Users need to adjust their analysis procedures to make use of new techniques.

In a paper presented in 1974 entitled "Bugs Money," Gilbert (1976) challenged entomologists to push pest research past population dynamics. He said, "We must also predict the effects of these pest populations upon vegetation.... What we are really concerned about is the effect on eventual yields." Gilbert's concerns are being met.

Acknowledgments

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[16] J. Barnard, phone conversation, July 17, 1984. Address: USDA Forest Service, Northeastern Forest and Range Experiment Station, 370 Reed Road, Broomall, PA 19008.

whom helped formulate many of the ideas presented here. Of course, I am responsible for the paper's contents.

Literature Cited

Alfaro, R.I.; Van Sickle, G.A.; Thomson, A.J.; Wegwitz, G. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Can. J. For. Res. 12:780-787.

B.C. Forest Service. 1977. Evaluation of the western spruce budworm problem in British Columbia. For. Prot. Div., B.C. For. Serv., Victoria, B.C. 153 p.

Bousfield, W.E. 1980. The effects of height growth loss on stands damaged by the western spruce budworm. U.S. Dep. Agric., For. Serv., Northern Reg., State and Priv. For., For. Insect and Dis. Manage., Missoula, MT. Rep. 80-11. 3 p.

Bible, T.D. 1985. Economic considerations for spruce budworm management in North America. Pages 176-187 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp. 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Bruhn, J.A. 1980. A stochastic model for simulation of daily weather. Prot. Ecol. 2:199-208.

Bruhn, J.A.; Fry, W.E.; Fick, G.W. 1979. WEATHER: a stochastic simulation model of daily weather. User's manual. Cornell Univ., N.Y. State Coll. Agric. and Life Sci., Dep. Plant Pathol., Ithaca, N.Y. Mimeo 79-2.

Carolin, V.M.; Coulter, W.K. 1975. Comparison of western spruce budworm populations and damage on grand fir and Douglas-fir trees. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-195. 16 p.

Colbert, J.J.; Campbell, R.W. 1978. The integrated model. Pages 216-230 *in* M.H. Brookes, R.W. Stark, and R.W. Campbell, eds. The Douglas-fir tussock moth: a synthesis. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1585.

Colbert, J.J.; Overton, W.S.; White, C. 1979. Documentation of the Douglas-fir tussock moth outbreak population model. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Gen. Tech. Rep. PNW-89. 85 p.

Colbert, J.J.; Sheehan, K.; Crookston, N.L. 1983. Supporting decisions on western spruce budworm in forest management using simulation models. Pages 99-105 *in* W.K. Lauenroth, G.V. Skogerboe, and M. Flug, egs. Analysis of ecological systems: state-of-the-art in ecological modeling. Symp. Proc. Third Int. Conf. on state-of-the-art in ecological modeling, Colo. State Univ., 24-28 May 1982. Elsevier Scientific Publishing Company, Amsterdam – Oxford – New York. 992 p.

Collins, D.G.; Sickle, G.A. 1978. Damage appraised cruises in spruce budworm defoliated stands of Douglas-fir in 1977. Can. For. Serv., Pac. For. Res. Centre, Victoria B.C. Inf. Rep. BC-P-19-1978.

Crookston, N.L.; Roelke, R.C.; Burnell, D.G.; Stage, A.R. 1978. Evaluation of management alternatives for lodgepole pine stands using a stand projection model. Pages 114-122 *in* D.L. Kibbee, A.A. Berryman, G.D. Amman, and R.W. Stark, eds. Theory and practice of mountain pine beetle management in lodgepole pine forests. Symp., Wash. State Univ., Pullman, Wash., 25-27 April 1978. College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow.

Crookston, N.L.; Stark, R.W. 1985. Forest-bark beetle interactions: stand dynamics and prognosis. *In* W.E. Waters, R.W. Stark, and D.L. Wood, eds. Integrated pest management in pine-bark ecosystems. John Wiley, New York.

Duff, G.H.; Nolan, N.J. 1953. Growth and morphogenesis in the Canadian forest species: I. The controls of cambial and apical activity in *Pinus resinosa* Ait. Can. J. Bot. 31:471-513.

Ferguson, D.E.; Crookston, N.L. 1984. User's guide to the regeneration establishment model — a stand prognosis model extension. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-161. 23 p.

Gilbert, A.M. 1976. Bugs money. Pages 147-151 *in* Proc. Symp. on the spruce budworm, 11-14 November 1974, Alexandria, Va. U.S. Dep. Agric., For. Serv., State and Priv. For., For. Insect and Dis. Manage., Washington, D.C. Misc. Publ. 1327. 188 p.

Gregg, T.; Wortendyke, J.; Twardus, D.; Wear, J. 1979. 1976 western spruce budworm loss assessment survey north-central Washington. U.S. Dep. Agric., For. Serv., For. Insect and Dis. Manage., State and Priv. For., Pac. Northwest Reg., Portland, OR. 26 p.

Hamilton, D.A., Jr.; Edwards, B.M. 1976. Modeling the probability of individual tree mortality. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-185. 22 p.

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of the western spruce budworm in the American northern Rocky Mountain area from 1922 through 1971. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-20. 144 p.

Kemp, W.P. 1983. The influence of climate, phenology, and soils on western spruce budworm defoliation. Univ. Idaho, Moscow, Idaho. Ph.D. dissertation. 143 p.

Moeur, M. 1981. Crown width and foliage weight of northern Rocky Mountain conifers. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-283. 14 p.

Monserud, R.A. 1978. Combining the stand prognosis and Douglas-fir tussock moth outbreak models. Pages 268-272 *in* Proc., Soc. Am. For. annual meeting; St. Louis, Mo. Soc. Am. For., Washington, D.C.

Monserud, R.A. 1980. Estimating the volume of top-killed trees with the Behre hyperboloid. Mitteilungen der Forstlichen Bundesversuchsanstalt, Vienna. 30:179-186. (Paper presented at IUFRO meeting of groups S4.01–S4.02, 10-14 September 1979, Vienna, Austria.)

Monserud, R.A.; Crookston, N.L. 1982. A user's guide to the combined stand prognosis and Douglas-fir tussock moth model. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-127. 49 p.

Mott, D.G.; Navin, L.P.; Cook, J.A. 1957. Radial growth in forest trees and the effects of insect defoliation. For. Sci. 3:286-304.

Seymour, R.S. 1985. Forecasting growth and yield of budworm-infested forests. Part I: Eastern North America. Pages 200-213 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp. 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Seymour, R.S.; Mott, D.G.; Kleinschmidt, S.M.; Triandafillou, P.H.; Keane, R. 1985. Green Woods Model — a forecasting tool for planning timber harvesting and protection of spruce-fir forests under attack by the spruce budworm. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-91. 38 p.

Sheehan, K.; Crookston, N.L.; Kemp, W.P.; Colbert, J.J. (In press). Modeling budworm and its hosts. Chapter 8 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, eds. Western spruce budworm. U.S. Dep. Agric., Washington, D.C. Tech. Bull. 1694.

Stage, A.R. 1973. Prognosis Model for stand development. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-137. 32 p.

Stage, A.R. 1975. Prediction of height increment for models of forest growth. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-164. 20 p.

Stage, A.R. 1978a. Modeling probability of outbreak occurrence and stand involvement. Pages 59-61 *in* M.H. Brookes, R.W. Stark, and R.W. Campbell, eds. The Douglas-fir tussock moth: a synthesis. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1585.

Stage, A.R. 1978b. Modeling the growth of host stands. Pages 21-23 *in* M.H. Brooks, R.W. Stark, and R.W. Campbell, eds. The Douglas-fir tussock moth: a synthesis. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1585.

Stage, A.R. 1978c. Model of long-range stand response. Pages 89-90 *in* M.H. Brookes, R.W. Stark, and R.W. Campbell, eds. The Douglas-fir tussock moth: a synthesis. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1585.

Stage, A.R. 1978d. Site and stand inventory. Pages 193-195 *in* M.H. Brookes, R.W. Stark, and R.W. Campbell, eds. The Douglas-fir tussock moth: a synthesis. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1585.

Stage, A.R. 1978e. The stand prognosis model. Pages 210-215 *in* M.H. Brookes, R.W. Stark, and R.W. Campbell, eds. The Douglas-fir tussock moth: a synthesis. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1585.

Stage, A.R.; Alley, J.R. 1972. An inventory design using stand examinations for planning and programming timber management. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. 17 p.

Stage, A.R.; Ferguson, D.E. 1982. Regeneration modeling as a component of forest succession simulation, Pages 24-30 *in* J.E. Means, ed. Forest succession and stand development research in the Northwest. Symp., Oreg. State Univ., Corvallis, OR., 26 March 1981.

Thomson, A.J. 1979. Evaluation of key biological relationships of western budworm and its host-trees. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Inf. Rep. BC-X-186. 19 p.

Thomson, A.J.; Van Sickle, G.A. 1980. Estimation of tree growth losses caused by pest activity. Can. J. For. Res. 10:176-182.

USDA Forest Service. 1977. Final Environmental Statement western spruce budworm plan. U.S. Dep. Agric., For. Serv., Northern Reg., Missoula, MT.

USDA Forest Service. 1979. Western spruce budworm amended final Environmental Statement Boise and Payette National Forests state and private cooperation. U.S. Dep. Agric., For. Serv., Intermt. Reg., Ogden, UT. 39 p.

USDA Forest Service. 1983. Environmental Assessment western spruce budworm management in northern Oregon. U.S. Dep. Agric., For. Serv., Pac. Northwest Reg., Portland, OR. 36 p.

USDA Forest Service. 1984. Environmental analysis western spruce budworm management in northeastern Oregon. U.S. Dep. Agric., For. Serv., Pac. Northwest Reg., Portland, OR. 68 p.

Van Sickle, G.A. (In press). Host responses. Chapter 5 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, eds. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1694.

Van Sickle, G.A.; Alfaro, R.I.; Thomson, A.J. 1983. Douglas-fir height growth affected by western spruce budworm. Can. J. For. Res. 13:445-450.

Williams, C.B., Jr. 1966. Differential effects of the 1944-56 spruce budworm outbreaks in eastern Oregon. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-33. 16 p.

Williams, C.B., Jr. 1967. Spruce budworm damage symptoms related to radial growth of grand fir, Douglas-fir, and Engelmann spruce. For. Sci. 13(3):274-285.

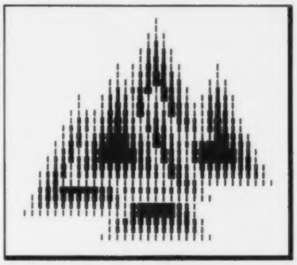
Wykoff, W.R.; Crookston, N.L.; Stage, A.R. 1982. User's guide to the Stand Prognosis Model. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-133. 112 p.

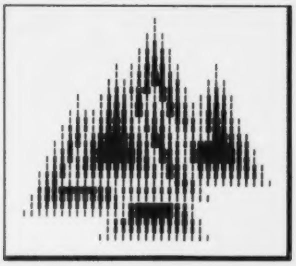
Wykoff, W.R. 1983. Predicting basal area increment for individual northern Rocky Mountain conifers. In: Mitteilungen der Forstlichen Bundesversuchsanstalt, Vienna. 147:127-143.

Workshop II —

Population and Impact Assessment

Are our current techniques adequate? What new or modified techniques are available for:





Workshop II — Population and Impact Assessment

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Thus far in the program, we have been given a great deal of information on the dynamics of budworm populations and their physical, ecological and socio-economic impacts on the forests. Numerous methods of population estimation and damage assessment have been alluded to, which were developed to support the particular lines of research described. A variety of analytical and predictive models intended to be useful to resource managers have been described, also.

But what about operational methods — methods of determining budworm densities and other quantitative population characteristics, methods of estimating damage and loss, and methods of estimating the effects of budworm activity on other forest parameters of concern — that are to be used in a budworm management program?

Are the methods now available adequate for all aspects of planning and decision-making? Most important, perhaps, do we have methods and procedures for obtaining the data required by the models that have been developed for operational budworm management systems?

These are the basic questions to be addressed in this workshop.

Jusqu'ici, nous avons reçu une masse de renseignements sur la dynamique des populations des tordeuses et sur leurs répercussions physiques, écologiques et socio-économiques sur la forêt. Il a été question de nombreuses méthodes d'estimation des effectifs et des dégâts, mises au point pour appuyer diverses orientations de la recherche, lesquelles ont été décrites. Une foule de modèles d'analyse et de prédiction destinés aux aménagistes des ressources ont aussi été décrits.

Mais qu'en est-il des méthodes opérationnelles (des méthodes de détermination de la densité et des autres caractéristiques chiffrables des populations de tordeuses, des méthodes d'estimation des dégâts, des pertes et des effets de la tordeuse sur d'autres paramètres forestiers intéressants) qui doivent toutes servir contre cet insecte?

Les méthodes actuellement proposées conviennent-elles à tous les aspects de la planification et de la prise de décisions? Point plus important peut-être, disposons-nous de méthodes et de procédés pour obtenir les données exigées par les modèles qui ont été mis au point pour la lutte opérationnelle contre les tordeuses?

Il s'agit de questions fondamentales auxquelles nous tenterons de répondre durant le présent atelier.

Use of the Overwintering- Larvae Soaking Method for Population Prediction in Maine

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Egg-mass sampling has been the preferred sampling technique for predicting population trends of spruce budworm (*Choristoneura fumiferana* (Clem.)) throughout the eastern United States and Canada (Dorais and Kettela 1982). In Maine, however, significant predictive errors were made in the late 1970s with egg-mass data as the sole base for prediction. Work is now underway in Maine to reduce predictive errors by improving the overwintering-larvae soaking method (L-II) (Miller et al. 1971) and adapting it to supplement or replace egg-mass sampling in Maine's spruce budworm survey.

The L-II method was initially used in Maine to supplement egg-mass sampling. L-II data predicted significantly different populations than egg-mass data, however. Paired egg-mass and L-II points showed poor correlation in early tests ($r^2 = 0.42$). When L-II predictions were compared directly to counts of needle-mining budworm in the spring (L-III), results were better ($r^2 = 0.68$).

Initial L-II tests in Maine were on fir, but as spruce protection became important, sampling was extended to red spruce. Counts on fir and red spruce at a point often showed wide variations. Tests comparing L-II counts on fir and red spruce with resulting L-III counts at the same point showed a better correlation ($r^2 = 0.76$) than when only fir counts were used. Underestimation of the population was sharply reduced when red spruce was included in the sample.

Tests in 1982 and 1983 used L-II counts of fir and red spruce and defoliation estimates on each species. Correlation of these data with L-III counts was better than all earlier comparisons ($r^2 > 0.80$).

The laboratory method was evaluated in 1982 and 1983. Initial tests showed poor extraction of larvae with the methods used in Maine since 1973. The extraction method accounted for about 40 percent of total larvae. Tests showed that NaOH concentrations, water temperature, and soaking time had minor effects on extraction, but bucket agitation and rinsing of foliage limited recovery. Constant agitation with a vibrating box and improved rinsing techniques improved extractions to greater than 85 percent of total larvae.

Technical and plumbing improvements in the Maine L-II facility have resulted in lower laboratory costs for L-II samples than for egg-mass samples.

Use of the L-II method in Maine is expanding. In 1983-84, most of the Maine budworm infestation was surveyed with the L-II method. Advantages of the method in Maine are:

- Recent tests and field use have shown L-II to be more accurate than egg-mass sampling in predicting populations in Maine.
- L-II samples are taken after fall dispersal of larvae, decreasing potential variability between tree species.
- Counting L-II larvae eliminates the problem of distinguishing new from old egg-masses.
- The L-II method can be used from mid-September through March, thus providing a much longer field season than with egg sampling. Field sample costs are about the same for the two methods.
- Laboratory costs per sample with L-II are about half egg-mass sampling costs.
- Spruce can be evaluated as easily as fir with the L-II method. Evaluating populations on spruce by egg-mass sampling is difficult.

Maine may soon use the L-II method exclusively for population prediction sampling. Work continues to improve the method. A sequential-counting method will be evaluated in 1984-85, and the potential for automated counting is being investigated.

Literature Cited

Dorais, L.; Kettela, E.G., compilers. 1982. A review of entomological survey and assessment techniques used in regional spruce budworm, *Choristoneura fumiferana* (Clem.), surveys and in the assessment of operational spray programs. Committee for the Standardization of Survey and Assessment Techniques, Eastern Spruce Budworm Council. Available from: Quebec Dep. of Energy and Resources, Gov. of Quebec, Quebec.

Miller, C.A.; Kettela, E.G.; McDougall, G.A. 1971. A sampling technique for overwintering spruce budworm and its applicability to population surveys. Can. For. Serv., Maritimes Forest Res. Centre., Fredericton, New Brunswick. Inf. Rep. M-X-25. 11 p.

Discussion Group A —
Determining Insect
Numbers

Sex Pheromone Traps for Monitoring Spruce Budworm Populations

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Sex pheromone traps are relatively cheap, efficient tools for monitoring the presence and abundance of insects.

For spruce budworm in the east, emphasis is on distributing traps before moth flight, and collecting them after. A "once-a-year" trap — to be distributed one year, and collected and replaced the next — is possible. To provide meaningful time-series data, the same trap design and type of dispenser must be used each year. Choosing correctly at the outset is essential.

Although early work in Ontario concentrated on sticky traps (Sanders 1978), they were unsuitable for sampling wide ranges of population densities because of trap-saturation (Houseweart et al. 1981). To avoid this problem, Ramaswamy and Cardé (1982) proposed a covered-funnel trap in which insects are killed by DDVP. This design was tested in Ontario in 1981, but moisture got into the traps and rotted the moths. A modified design, the double-funnel trap, was tested in 18 plots in Ontario in 1982 and 1983. Regressions of larval density *vs.* moth catch within the same generation gave R^2's of 77 and 51 percent for 1982 and 1983, respectively, and 62 percent for 1983 larvae *vs.* 1982 moth catch (Sanders 1984). In 33 plots, the Forest Insect and Disease Survey in Ontario in 1983 obtained R^2's of 40 percent for larvae *vs.* moth catch, 41 percent for egg masses *vs.* moths, and 44 percent for defoliation *vs.* moths. In view of the inaccuracies inherent in sampling larvae and egg masses, particularly at low population densities, these R^2's are reasonable.

Because the use of commercial traps is convenient in a long-term program in different Canadian Forest Service regions and parts of the United States, field and laboratory studies have evaluated four commercial designs: International Pheromone Limited, Uni-Trap; Health-chem gypsy moth canisters and milk-cartons; and Baker Chemicals, Bag-a-Bug (Sanders, 1985). Of these, the International Pheromone Limited Uni-Trap appears best, but recommendations must await more extensive field tests in 1984.

The main feature required of a lure is a known, constant release rate for the 6-week exposure period. Home-made polyvinyl chloride lures (PVC) have proved satisfactory for many years (Sanders 1981). Again, using commercially available lures is convenient, and comparative testing of three — Bend, Conrel hollow fibres, and Hercon flakes — is underway (Sanders 1984).

Sex pheromone traps can provide three types of information of use for managing spruce budworm damage.

- Time-series data indicating long-term trends.
- Early warning of threatening population increases (a development of time-series data).
- Estimation of insect abundance, to supplement or replace existing sampling techniques.

Full potential will depend on acceptance by users and development by the users to meet regional needs. Standardization of trap design and deployment is desirable, however, to facilitate comparison between jurisdictions.

Literature Cited

Houseweart, M.W.; Jennings, D.T.; Sanders, C.J. 1981. Variables associated with pheromone traps for monitoring spruce budworm populations (Lepidoptera: Tortricidae). Can. Entomol. 113:527-537.

Ramaswamy, S.B.; Cardé, R.T. 1982. Non-saturating traps and long-life attractant lures for monitoring spruce budworm males. J. Econ. Entomol. 75:126-129.

Sanders, C.J. 1978. Evaluation of sex attractant traps for monitoring spruce budworm populations (Lepidoptera: Tortricidae). Can. Entomol. 110:43-50.

Sanders, C.J. 1981. Release rates and attraction of PVC lures containing synthetic attractant of the spruce budworm, *Choristoneura fumiferana*. Can. Entomol. 113:103-111.

Sanders, C.J. 1984. Sex pheromone traps and lures for monitoring spruce budworm populations — the Ontario experience. *In* D. Grimble and D. Kucera (Chairmen). Proc. New and improved techniques for monitoring and evaluating spruce budworm populations. U.S. Dep. Agric., For. Serv., Northeast. For. and Range Exp. Stn., Broomall, PA. Gen. Tech. Rep. NE-88.

Sanders, C.J. 1985. The role of sex pheromone traps in coping with the spruce budworm. *In* D. Schmidt, ed. Spruce-fir management and spruce budworm. Proc. Soc. Am. For. Tech. Conf. VI, Burlington, VT. U.S. Dep. Agric., For. Serv. Northeast. For. and Range Exp. Stn., Broomall, PA. Gen. Tech. Rep. NE-99. 217 p.

Sampling Larvae of the Western Spruce Budworm

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Classification schemes have been developed for separating light from moderate-to-heavy and light-to-moderate from heavy populations of fourth instars. To use the plan in well-defined entomological units of forest area, samples must be obtained from representative parts of the units. The number of subunits needed within a unit is based primarily on the availability of workers and other resources. Enough subunits should be established to ensure that they are representative of the entomological unit (Srivastava and Campbell, in press).

The sequential count plan for fourth-instar larvae is similar to the classification scheme, except that it provides a density estimate per sample unit at specified precisions (Twardus, in press). To use this plan in small homogenous areas, one should fix a precision level, randomly select about 25 to 30 trees and then sample a 45-cm terminal tip from the mid-crown of each tree. Sampling continues until the total number of larvae exceeds a specified number contingent on the number of trees sampled and precision desired (Srivastava and Campbell, in press). Plans are presented for sampling precisions of 15, 20, and 25 percent (Twardus, in press). The number of sample trees usually increases as population density decreases.

Campbell et al. (1983) have determined the within-tree distribution of fourth-instar larvae from densities found on terminal 45-cm tips of branches drawn from the upper, mid, and lower crowns of host trees in Washington, Oregon, and Montana (Campbell and Srivastava, in press). The number of larvae on each tip are converted to density per square metre of foliage. Density of fourth instars per square metre of foliage on mid-crown terminal tips was usually between density in the upper and lower crown. In most cases densities on average trees were highest in the upper crown third and lowest in the lower third. These results confirm that mid-crown density on terminal tips is a good predictor of density in both the upper crown and the lower crown, and hence a good predictor of average density in the whole tree (Campbell et al., 1983). Moreover, at least for the populations studied, whole-plot and whole-stand densities of the western spruce budworm (fourth instars, pupae, pupal exuviae, and egg masses) can be estimated from terminal-tip densities from a single third of the tree crown (Srivastava et al., 1984).

Most resource managers are currently interested in approaching the western spruce budworm problem through judiciously managing the forest. To implement appropriate silvicultural practices or direct suppression tactics, managers need to know about the processes that maintain populations at both high and low densities and the processes that upset population stability and lead to outbreaks (Srivastava and Campbell, in press).

Accurate estimates of pest density — rather than mere broad classifications — may be important in reaching rational treatment decisions. These estimates are contingent on a clear definition of the sampling universe and its bounds — whether a forest stand, a valley or drainage, or an entomological unit. Moreover, larval densities or aggregative patterns differ among branches, vertical crown strata, tree heights, host species, and phases of infestation (Campbell and Srivastava, in press). Accurate estimates are sometimes difficult because managers do not have the resources to apply traditional sampling schemes (Srivastava et al. 1984; Twardus, in press).

For about 10 days, populations are relatively stable when larvae — primarily third and fourth instars — are in expanding buds. This period is good for sampling because larvae are webbed in their feeding sites but still active and easy to find. Because bud development differs among stands and between hosts, timing of sampling is critical to ensure comparability of data among all of the trees or areas sampled (Twardus, in press).

Western researchers have developed a sequential-sampling plan for classifying western spruce budworm populations in terms of expected defoliation by sampling fourth instars. Sequential-count plans have also been developed for fourth instars, residual pupae (those remaining after predation), and egg masses by Srivastava and Campbell (in press).

To classify expected defoliation using fourth-instar density, 45-cm terminal tips are sequentially sampled from the mid-crown of each tree in a stand until the cumulative number of larvae falls within a predetermined threshold (Twardus, in press):

Number of larvae per 45-cm tip	*Infestation class*
0-3	*Light*
4-7	*Moderate*
8	*Heavy*

Among the western spruce budworm populations recently studied in the Northwest, fourth-instar densities ranged from about 0.3 to 80 larvae per square metre, with the highest recorded density of 160 fourth instars per square metre. However, fourth-instar densities greater than about 100 larvae per square metre have rarely been found either in the Pacific Northwest or in northern New Mexico. Populations of the eastern budworm commonly exceed 80 larvae per square metre and late larval survival increases slightly to about 140 fourth instars per square metre. If this major apparent difference between the numerical behavior of the two budworm species proves to be general, it should provide much of the basis for understanding both the relatively indeterminate duration of outbreaks by the western species and the relatively mild biological effects of those outbreaks, compared to the eastern budworm (Campbell, in press).

For population research, the sampling schemes discussed should provide precise estimates with minimum effort. For survey work, the sequential schemes appear to provide forest-pest managers an alternative for estimating larval densities at prescribed precisions, at a fraction of the cost of traditional fixed-size sampling schemes (Srivastava and Campbell, in press).

Literature Cited

Campbell, R.W. (In press). Population dynamics. Chapter 6 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, eds. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1695.

Campbell, R.W.; Srivastava, N. (In press). Distributions of the western spruce budworm (Lepidoptera: Tortricidae). Environ. Entomol.

Campbell, R.W.; Srivastava, N.; Torgerson, T.R.; Beckwith, R.C. 1983. Patterns of occurrence in western spruce budworm (Lepidoptera: Tortricidae). Environ. Entomol. 13(2):533-530.

Srivastava, N.; Campbell, R.W. (In press). Sequential classification and count plans for the western spruce budworm (Lepidoptera: Tortricidae): egg masses, instar IV and pupae. Environ. Entomol.

Srivastava, N.; Campbell, R.W.; Torgerson, T.R.; Beckwith, R.C. 1984. Sampling the western spruce budworm; fourth instars, pupae, and egg masses. For. Sci. 30(4):883-892

Twardus, D.B. (In press). Surveys and sampling and sampling methods for population and damage assessment. Chapter 5 *in* M.H. Brookes, R.W. Campbell, R.W. Stark, J.J. Colbert, R.G. Mitchell, eds. Managing trees and stands susceptible to western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1696.

Discussion Group A —
Determining Insect
Numbers

Prototype II Detector-Counter for Egg Masses of Spruce Budworm

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To determine population trends and forecast damage, many federal and state agencies spend tens of thousands of dollars each year sampling egg masses of the spruce budworms, both *Choristoneura fumiferana* (Clem.) and *C. occidentalis* Freeman, and the jack pine budworm (*C. pinus pinus* Freeman). Collecting foliage samples is difficult and requires specialized equipment (Morris 1955; Stein 1969). Once collected, the foliage is examined in the laboratory by trained examiners, but the examination process is tedious, time consuming, and subject to human error. Accuracy is related to budworm population density, the nature of the foliage, and worker experience (Morris 1951, 1955).

Both accuracy and efficiency of foliage examinations can be improved by examining branches under black light (Jennings 1968; Acciavatti and Jennings 1976). Egg masses of the spruce budworm, the western spruce budworm, and the jack pine budworm fluoresce when excited by longwave ultraviolet (UV) light. The excitation wavelength extends from 300 to 400 nanometres (nm).

A study at the University of Maine (Departments of Physics and Astronomy, Electrical Engineering, and Entomology in collaboration with the Northeastern Forest Experiment Station) indicated that fluorescing properties of budworm egg masses can be used to detect and count egg masses electronically. A Prototype I counter was built and tested at the University of Maine. Test results of Prototype I indicated that manual counts can be predicted ($R^2 = 0.9$, $\alpha = 0.01$) from electronic count, and electronic counting showed a highly significant ($\alpha = 0.01$) reduction in processing time: manual examinations $\bar{x} = 29.5$ min/branch; electronic examination $\bar{x} = 8.6$ min/branch.

To incorporate new electronic hardware and expand operating potential, a new egg-mass detector and counter (Prototype II) was designed and developed at the USDA Forest Service, Missoula Equipment Development Center (MEDC), Fort Missoula, Montana (Figure 1). New design features include: a variable optical-scanning system to detect egg-mass fluorescence of both spruce budworm and western spruce budworm; programmable "windows" for setting maximum-minimum detection levels and for screening fluorescing components on five host species; a stepper motor with variable belt-drive system; and a programmable microprocessor for operation and maintenance. Prototype II is currently undergoing an operational test at MEDC, in cooperation with the Methods Application Group (MAG); Forest Pest Management, R-1, R-2, R-3; CANUSA-East and CANUSA-West; and the Northeastern Forest Experiment Station.

Figure 1. Prototype II spruce budworm egg mass detector-counter.

Literature Cited

Acciavatti, R.E.; Jennings, D.T. 1976. Locating western spruce budworm egg masses with ultralight light. U.S. Dep. Agric., For. Serv., Rocky Mt. For. and Range Exp. Stn., Fort Collins, CO. Res. Note RM-313. 3 p.

Jennings, D.T. 1968. Using black light to find jack-pine budworm egg masses. U.S. Dep. Agric., For. Serv., North Central For. and Range Exp. Stn., St. Paul, MN. Res. Note NC-56. 3 p.

Morris, R.F. 1951. One source of error in budworm population work. Can. Dep. Agric., Div. For. Biol. Bi-Mon. Prog. Rep. 7(6):1-2.

Morris, R.F. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. Can. J. Zool. 33:225-294.

Stein, John D. 1969. Modified tree-pruner for twig sampling. U.S. Dep. Agric., For. Serv., Rocky Mt. For. and Range Exp. Stn., Fort Collins, CO. Res. Note RM-130. 2 p.

Discussion Group A —
Determining Insect
Numbers

Spruce Budworm Sampling to Forecast Populations in Quebec

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Three techniques are used in the province of Quebec to sample spruce budworm populations: egg-mass surveys, second-instar larval surveys, and adult surveys (pheromone traps). The egg-mass and second-instar larval surveys have been modified over the past few years to improve efficiency.

Changes to the egg-mass survey include a new method for evaluating egg masses on branch surfaces, which involves measuring the total length then multiplying by the total width to develop a cumulative total per area. Also in the early 1970s, all data were accumulated in the field, but now after collection of branches, data are processed in a central laboratory to obtain estimates of defoliation, egg mass counts, and information on hibernation sites. Egg mass counts are verified systematically by experienced personnel.

Egg-mass surveys are now used to obtain an early estimate of expected spruce budworm populations. Areas with populations are then subsampled for second-instar larvae. Also all areas that are to be sprayed the following year are surveyed for second-instar larvae and spray boundaries are adjusted, based on the results.

We have concluded that egg-mass surveys tend to underestimate increasing budworm populations and overestimate populations during collapse of an infestation, but are reasonably accurate for forecasting epidemic populations. In general, about 15 to 25 percent of egg masses are missed by observers on the first count. The proportion of unobserved egg masses varies from one observer to another, dependant on the time of day, type of branch, population level, and several other factors. The cost of egg mass surveys has averaged $105 CAN. per sample location.

Second-instar larval surveys have been an integral part of spruce budworm forecasting in Quebec since 1978. Improvements made in processing of the technique have reduced the cost of sampling second-instar larvae to $80 CAN. per sample location. In addition to the lower cost per sample location as compared to egg-mass surveys, we have found that estimates are more accurate than those based on egg mass counts. Second-instar surveys have therefore replaced egg-mass surveys for sampling within areas of known infestations.

Surveys of adult spruce budworm populations with pheromone traps have been used in Quebec for several years, primarily to complement egg mass counts and second-instar larval surveys in forecasting movements of spruce budworm populations. Pheromone traps have proved useful in several ways. For example, negative results from an adult survey would indicate no other surveys were needed at that location. On the other hand, a high adult population could indicate that an intensive egg mass count or second-instar larval survey was not needed that year, but the high adult population could foretell a potential population increase the following year. In such a case, egg-mass and second-instar larval surveys would be concentrated in that location to monitor the anticipated increase in budworm infestation.

Research conducted in recent years under the CAN-USA Program and by the Canadian Forestry Service has led to measurable improvements in the adult spruce budworm survey technique toward developing its potential for population forecasting and population dynamics studies as well as its current use as an additional means for detecting population trends of the spruce budworm.

Discussion Group A — Determining Insect Numbers

Use of Pheromone-Baited Traps to Monitor Populations of Spruce Budworm

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The availability of a reliable and practical technique to monitor populations of spruce budworm (*Choristoneura fumiferana* (Clem.)) is necessary for responsible management of eastern spruce-fir forests. Knowledge of budworm population trends and expected damage is essential to prevent crises and reduce the probability of future economic losses. Methods currently used to estimate the abundance of pre-adult life stages of *C. fumiferana* (Allen et al. 1984) adequately detect population trends and predict damage, but their cost in time and money limit their use. Another shortcoming of currently applied techniques is that lack of standardization makes it difficult to compare monitoring results between regions. Practitioners seem reluctant to adjust their methods in the interest of standardization.

The objective of our field trials of pheromone-baited traps was to apply currently available knowledge and tools to develop a reliable, practical and standardized technique for monitoring sparse to medium density spruce budworm populations.

Procedures used in the 3-year (1981-1983) field trials (Abrahamson et al. 1984) and a recommended application of methods (Allen et al. 1984) were discussed at a previous symposium.

Preliminary results indicate that in the near future pheromone traps baited with spruce budworm pheromone can be used to: 1) detect the presence of budworm, 2) document the occurrence and location of interregional dispersal flights, 3) compare relative abundance of budworm in different forest stands, 4) predict population trends in stands where low budworm densities preclude practical application of other monitoring techniques, and 5) provide a reliable means to predict larval density.

The ability to predict future larval density (i.e., instar II or instars III-IV in generation n + 1) based on moth catch in pheromone-baited traps, constitutes the most precise application of this monitoring tool. Pooled 1983 data (N = 74-98 five-trap clusters) from plots in five northeastern states and two eastern Canadian provinces provided significant ($P < 0.05$) and encouraging coefficients of determination (i.e., $r^2 > 0.50$) for larval density *vs.* mean number of spruce budworm moths caught per trap. The object of 1984 field trials was to improve correlations through emendations in trap design, more extensive larval sampling in each plot, and utilization of a minimum of 15 plots in each region. Results from initial trials indicated that the latter is necessary because of regional differences in forest biotypes, climate and budworm history. Analysis of 1982-83 data by region, for example, significantly improved some coefficients of determination for 1982 mean trap catch vs. 1983 L3-L4 density (New Hampshire – $r^2 = 0.64$, N = 9; Newfoundland – $r^2 = 0.84$, N = 7).

Literature Cited

Abrahamson, L.P.; Allen, D.C.; Lanier, G.N. 1984. Application of pheromone traps to effectively monitor spruce budworm populations. Pages 13-16 *in* D. Grimble and D. Kucera (Chairmen). Proc. New and improved techniques for monitoring and evaluating spruce budworm populations. U.S. Dep. Agric., For. Serv., Northeast For. and Range Exp. Stn. Broomall, Pa. Gen. Tech. Rep. NE-88.

Allen, D.C.; Dorais, L.; Kettela, E.G. 1984. Survey and detection. Pages 22-36 *in* D.M. Schmitt, D. Grimble, and J.L. Searcy, Tech. Coords. Managing the spruce budworm in eastern North America. U.S. Dep. Agric., Agric. Handb. 620. Washington, D.C.: Canada/United States Spruce Budworms Program.

Allen, D.C.; Abrahamson, L.P.; Lanier, G.N. 1984. Monitoring spruce budworm populations with pheromone-baited traps. Pages 23-24 *in* D. Grimble and D. Kucera (Chairmen). Proc. New and improved techniques for monitoring and evaluating spruce budworm populations. U.S. Dep. Agric., For. Serv., Northeast For. and Range Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-88.

Discussion Group A — Determining Insect Numbers

Moth Captures in Pheromone-Baited Traps relative to Subsequent Defoliation of Douglas-fir by Western Spruce Budworm

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The objectives of our study were to determine the optimum bait strength needed for sticky traps so that tending through the flight season would not be necessary, to determine the relationship between trap catch and subsequent defoliation, and to determine the optimum allocation of traps in operational surveys according to cost and reliability specifications.

Cost-effective surveying of extensive areas requires an inexpensive trap that can be easily assembled, transported, installed, retrieved, and processed. Ideally, such a trap would operate through the flight season without servicing. Based on previous work a sticky trap made of a 2-litre milk carton seemed to meet these practical requirements. A basic problem with sticky traps is that they saturate with captured moths if the bait is too strong. Our approach in dealing with the saturation problem has been to test progressively weaker baits.

The experimental design used for trapping in 1981 and for estimating defoliation in 1982 was:

Sampling Unit	*No. Traps/Bait*	*No. Trees/Defoliation*
Stand	3	9
Cluster	9	27
Area	27	81

Traps within a *stand* were spaced at least 30 m (98 ft) apart. Generally, stands within a *cluster* were separated by 1 km (0.6 mi.), and clusters within an *area* by 5 km (3 mi.). Nominally, areas were 1 000–10 000 ha (2,471–24,710 acres) in size.

All baits were 3 × 5 mm pellets of plastic (polyvinyl chloride) impregnated with a 92:8 blend of (E)-11 and (Z)-11 tetradecenal. Their strengths are here expressed as percent pheromone of bait weight. Hourly, the release rate of a 0.01 percent bait approximates an average virgin female. Baits in 1981 contained 0.01, 0.001, and 0.0001 percent pheromone by weight. Traps were placed in early July and retrieved in late August.

Defoliation was assessed in the subsequent year by cutting 4 sample branches per tree and categorizing 25 new shoots per branch according to a six-class scale widely used in the western United States: 0 = no defoliation, 1 = 1-25 percent, 2 = 26-50 percent, 3 = 51-75 percent, 4 = 76-99 percent, and 5 = 100 percent.

The results we obtained are summarized in the following tables:

Optimum Bait Strength

Area	*Moths/trap by bait strength* 0.01	0.001	0.0001	*Subsequent defoliation*
Ukiah	82	73	58	*severe*
Hermiston	59	59	41	*moderate*
Warm Springs	75	55	19	*light*

Trap Catch with 0.0001 percent Baits in 1981 Relative to 1982 Defoliation

Sampling Unit	*No. Units*	*Traps/Unit*	*R2*
Stand	27	3	0.76
Cluster	9	9	0.94
Area	3	27	0.98

We concluded that sticky traps with 0.0001 percent baits can be used to index moth populations in an area when placed before the onset of moth flight and operated without tending until retrieved at end of the flight season. Furthermore catches of moths in traps with 0.0001 percent baits were highly correlated with severity of defoliation in the subsequent year, and the average defoliation in areas covering 1 000–10 000 ha (2,471–24,710 acres) can be predicted reliably with as few as 9 traps.

Discussion Group A —
Determining Insect
Numbers

Developing Improved Egg Mass Sampling Methods for the Lake States Region

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Field and laboratory analytic studies of spruce budworm egg mass numbers and distributions has led to the following observations when considering sampling in mixed spruce-fir stands in the Lake States:

1. Considerable tree-to-tree and cluster-to-cluster variation;
2. The average egg mass density in spruce trees may be considerably higher than that in balsam fir trees; for the low density populations sampled in this study, the ratio of white spruce to balsam fir density varied from 2 to 4.2 with an average of 2.91;
3. The branch-to-branch, tree-to-tree, and cluster-to-cluster variation of density may be considerably higher in white spruce compared to balsam fir trees; for the low density populations sampled in this study, the tree-to-tree variance for white spruce was approximately 9 times as large as that for balsam fir;
4. The biases due to using whole branches as the sampling unit with simple random sampling are relatively small;
5. The per branch mean and variance of egg mass density at mid-crown is, in general, lower than that for the tree without top;
7. The per branch variance of egg mass density for feasible branches increases as branch size decreases and is larger than the variance of a tree without top for smaller branch sizes;
8. The egg mass density of feasible branches is higher than that of a tree without top with the difference increasing as branch size decreases;
9. There may be a relatively strong positive linear correlation between white spruce and balsam fir egg mass density; for the five low-density clusters sampled in this study, the linear correlation coefficient was 0.71;
10. The most precise and accurate estimates of total egg mass density for white spruce are obtained from samples of whole feasible branches;
11. The most precise and accurate estimates of total egg mass density for balsam fir are obtained by selecting whole branches from each of the lower- and mid-crowns, but sampling whole feasible branches is almost as accurate and precise;
12. The distortion of probability statements caused by sampling whole feasible branches to estimate total egg mass density is relatively small — this distortion is moderate when sampling branches from each of the lower- and mid-crowns;
13. Sampling whole branches from the lower- and mid-crowns yields estimates of total egg mass density that are more precise and accurate than estimates based on sampling whole branches at mid-crown;
14. Sampling should not be done in the upper-crown;
15. The optimum sample unit is a whole feasible branch.

These results have led to the development of specific survey sampling procedures for the Lake States. Among the recommendations are 1) using permanent sampling locations, 2) establishing at least two stations per county, and 3) designating a monitoring location as being a cluster of five plots, each plot being monitored yearly.

Literature Cited

Fowler, G.W.; Simmons, G.A. 1982. Spruce budworm egg mass density on balsam fir: low to very high levels. Great Lakes Entomol. 15:277-286.

Fowler, G.W.; Simmons, G.A. 1984. Considerations when sampling spruce budworm egg masses on balsam fir and white spruce in the Lake States: low population levels. Great Lakes Entomol. 17:97-109.

Fowler, G.W.; Simmons, G.A. 1984. Sampling procedures for spruce budworm egg mass surveys (with reference to the Lake States). U.S. Dep. Agric. For. Serv., Washington, D.C. Agric. Handb. 635.

Simmons, G.A.; Fowler, G.W. 1982. Spruce budworm egg mass density on balsam fir and white spruce: low population levels. Great Lakes Entomol. 15:287-296.

Simmons, G.A.; Fowler, G.W. 1984. Considerations when sampling spruce budworm egg masses on balsam fir in the Lake States: low to extreme population levels. Great Lakes Entomol. 17:87-95.

Discussion Group A —
Determining Insect
Numbers

Determining Population Density of Spruce Budworm Larvae in Eastern North America

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During the past 40 years in eastern North America, either whole branch or 45-cm branch tip sample units from a host tree have been collected to determine population density of the spruce budworm (*Choristoneura fumiferana* (Clem.)) depending on the stadium under investigation (Sanders 1980). Feeding larval populations (second-to sixth instars) are primarily static and cause damage to trees. Therefore, these stages have provided a sound basis with which to compare annual fluctuation in density estimates and to evaluate the incidence of parasitism and/or disease. Sampling egg masses and dispersing first- or second-instar larvae has proven to be more difficult and tedious.

For intensive research on the biology and population dynamics of the spruce budworm, sampling several crown strata has been recommended, which is feasible at moderate to high densities (Morris 1955). At low densities, however, most researchers rely on a single, 45-cm branch tip from the mid-crown of the host tree (Dobesberger and Lim 1983; Régnière and Sanders 1983). Mathematical modeling of spruce budworm numbers requires a measure of reliability defined in statistical terms by the desired level of precision and confidence sought. Sample estimates of mean density and variance for larval populations based on the negative binomial distribution with a common k (Dobesberger and Lim 1983) and a density-dependent k (Dobesberger, in press), regression of mean crowding, $\mathring{m}$ as a function of mean density, m (Régnière and Sanders 1983; Dobesberger, in press), and Taylor's Power Law (Dobesberger, in press) to determine this reliability, have yielded large estimates or sample variance which suggest that the branch tip sample unit may not be appropriate. As Régnière and Sanders (1983) point out, the search for an alternate expression of density or sample unit would be useful. An expression of feeding larval density as number per unit dry weight of foliage might be most appropriate because such a sample unit could be related to the known theories of individual tree and stand growth (Dobesberger 1981). By examining the components of growth of the apically dominant host species of the spruce budworm, it should be possible to coordinate an effective integration of compatible spruce budworm and forest stand population dynamics models.

Literature Cited

Dobesberger, E.J. (In press.) Comparison of methods to determine required sample size for spruce budworm, *Choristoneura fumiferana* (Clem.), populations in Newfoundland. Can. Entomol.

Dobesberger, E.J. 1981. Crown dynamics in *Pinus resinosa* Ait.: Analysis and stochastic description of branch production, branch extension growth and foliage dry weight – branch length relationships. M. Sc. F. Thesis, Lakehead University, Thunder Bay, Ontario, 128 p.

Dobesberger, E.J.; Lim, K.P. 1983. Required sample size for early instar larvae of spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), in Newfoundland. Can. Entomol. 115:1523-1527.

Morris, R.F. 1955. The development of sampling techniques for forest insect defoliators, with particular reference to the spruce budworm. Can. J. Zool. 33:225-294.

Régnière, J.; Sanders, C.J. 1983. Optimal sample size for the estimation of spruce budworm (Lepidoptera: Tortricidae) populations on balsam fir and white spruce. Can. Entomol. 115:1621-1626.

Sanders, C.J. 1980. A summary of current techniques used for sampling spruce budworm populations and estimating defoliation in eastern Canada. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont., Inf. Rep. O-X-306, 33 p.

Discussion Group A —
Determining Insect
Numbers

Development of a Large-Capacity Pheromone Trap for Monitoring Forest Insect Pest Populations

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In 1982, research was initiated to design a large-capacity, pheromone-baited trap that would incorporate features leading to the production of a commercial trap for detecting and monitoring forest insect pests such as the spruce budworm (*Choristoneura fumiferana* (Clem.)). A standard-design trap for several insect pests would ultimately result in greater use and lower production costs.

The trapping efficacy of the "home-made" nonsaturating pheromone vertical trap (PTV) was field-tested in stands with high spruce budworm populations in 1982 and compared with a cover funnel trap (CFT) developed by Ramaswamy and Cardé (1982). In 1983, investigations were conducted to measure the influence of location on the efficacy of PTV traps in balsam fir stands that had low budworm populations. The PTV trap was commercially produced in 1984 under the trade name of Multi-Pher® and its efficacy compared in the field to a trap produced by International Pheromones Ltd., Warrington, England, for trapping stored-products moths (S.P.I.® Moth Trap).

The PTV trap (Figure 1a), and the resulting commercially produced Multi-Pher® (Figure 1b), have a large container section attached under a rain and debris shield with entry ports and funnel. A complete description of both traps will be published elsewhere. The Multi-Pher® trap has a removable metal hook attached to its cover which allows the trap to be fixed on a branch in the tree crown using a long pole. A solid polyvinyl chloride (PVC) plastic pellet containing 0.03 conc. of Fulure is used as bait. In 1982, five plots were used for mid-crown trials and six plots were used for near-ground trials in stands with high budworm populations. Two plots were used in 1983 to study border effects; five plots were used in 1984 for mid-crown and near-ground trials to compare Multi-Pher® and S.P.I.® traps. In all plots, traps were set in two parallel lines at a distance of 40 m (131 ft) between lines and traps.

In 1982, the PTV (home-made) traps retained 86.4 percent of the total number of male moths captured in the lower mid-crown section and 77.5 percent at 2 m (6 ft) from the ground as compared to 13.6 and 22.5 percent respectively for CFT traps. Testing differences among means, we found that the PTV trap is more efficient ($P<0.01$) and a comparison of coefficient of variation (Table 1) indicates less variation in PTV than in CFT traps. From results of location on trees, PTV trap efficacy (Table 2), shows that 50.1 percent of moths captured were collected by traps in the mid-crown section of trees located on roadsides and significant

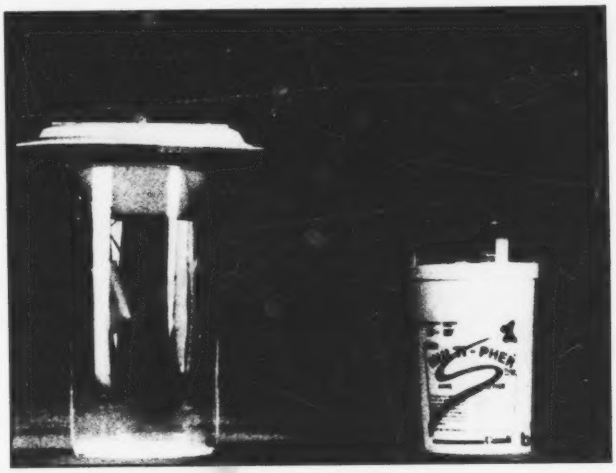

Figure 1. The prototype PTV pheromone trap (a) and the resulting commercial Multi-Pher® trap (b) for spruce budworm population monitoring.

Table 1
Spruce budworm male moths collected in two nonsaturating pheromone traps in 1982

Trapping location	*Trap type*	*Number of traps*	*Number of SBW male moths/trap*					*Average number of males (%)*
			Min.	*Max.*	*X*	*S*	*C.V.*	
Mid-crown	*CFT*	*10*	*464*	*1372*	*786*	*263.2*	*0.33*	*13.6*
	PTV	*15*	*3012*	*6802*	*4994*	*1189.8*	*0.24*	*86.4*
Ground (2 m)	*CFT*	*12*	*252*	*626*	*436*	*107.8*	*0.25*	*22.5*
	PTV	*18*	*1033*	*1782*	*1502*	*349.1*	*0.23*	*77.5*

differences (P<0.01) were observed between traps located in mid-crown and those located at the three other sampling locations studied. The Multi-Pher® trap was significantly more efficient (P<0.05) than the S.P.I.® trap located either in the tree crown or near ground level (Table 2).

Following on the 1982-1983 results, the Ministry of Energy and Resources of Quebec decided to establish, in 1984, a spruce budworm monitoring system across the province of Quebec (Figure 2). Three Multi-Pher® pheromone traps baited with PVC at 0.03 conc. of Fulure were used in each of 165 plots located in balsam fir-spruce stands susceptible to budworm attack; results (Table 3) will be published in detail later.

Literature Cited

Ramaswamy, S.B.; Cardé, R.T. 1982. Nonsaturating traps and long-life attractant lures for monitoring spruce budworm males. J. Econ. Entomol. 75:126-129.

Table 2
Spruce budworm male moths collected in PTV traps located in mid-crown and near-ground sites in the forest (inner) and on roadside (border) in 1983

Trapping location	*Number of traps*	*Number of SBW male moths/trap*						*Average number of males (%)*
		Min.	*Max.*	*X*	*S*	*C.V.*	*	
Mid-Crown	*12*	*534*	*1871*	*1193*	*484.1*	*0.41*	*A*	*50.1*
Border								
Inner	*12*	*183*	*1174*	*619*	*301.7*	*0.49*	*B*	*26.0*
Ground (2 m)	*12*	*166*	*907*	*398*	*240.2*	*0.60*	*B*	*16.7*
Border								
Inner	*12*	*50*	*298*	*170*	*79.1*	*0.46*	*C*	*7.2*

* P<.01 Any two means not identified by the same letter are significantly different.

Table 3
Spruce budworm male moths captured in three Multi-Pher® and three S.P.I.® traps in each of five sites established along roadsides in 1984

Trapping location	*Trap type*	*Number of SBW male moths/trap*					*Average number of males (%)*
		Min.	*Max.*	$\overline{X}$	*S*	*C.V.*	
	*M.-P.**	*98*	*112*	*106*	*7.4*	*0.07*	*69.0*
	*S.P.I.***	*44*	*72*	*56*	*14.4*	*0.26*	*30.9*
	M.-P.	*194*	*339*	*264*	*72.6*	*0.27*	*67.8*
	S.P.I.	*92*	*139*	*114*	*23.5*	*0.20*	*32.2*
Ground (2m)	*M.-P.*	*250*	*318*	*268*	*43.5*	*0.16*	*65.1*
	S.P.I.	*134*	*142*	*157*	*34.3*	*0.22*	*34.9*
	M.-P.	*616*	*869*	*735*	*127.1*	*0.17*	*69.8*
	S.P.I.	*267*	*402*	*313*	*76.5*	*0.24*	*30.2*
Mid-Crown	*M.-P.*	*153*	*222*	*177*	*38.7*	*0.22*	*79.7*
	S.P.I.	*39*	*70*	*51*	*16.6*	*0.33*	*20.3*

* Multi-Pher® Trap.
** Stores-Products Insect® Moth Trap.

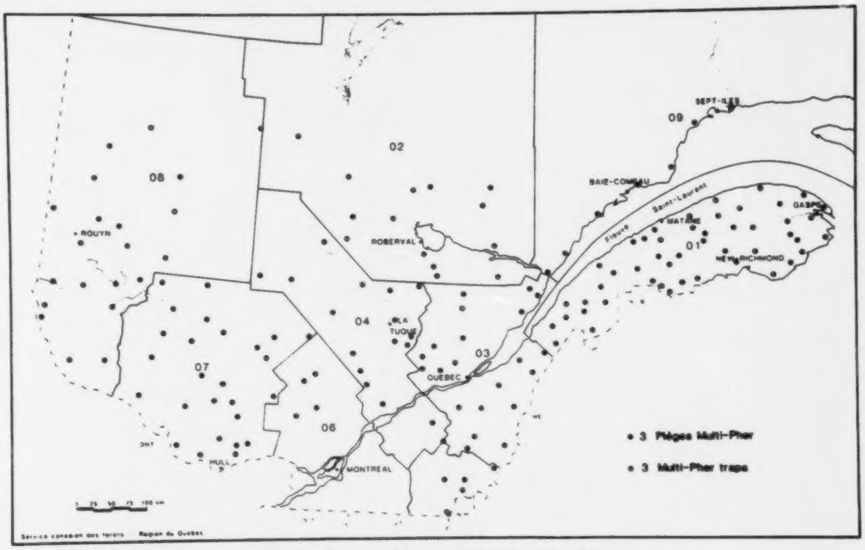

Figure 2. Spruce budworm monitoring system established by the Ministry of Energy and Resources of Quebec in 1984 using Multi-Pher® traps.

Discussion Group A — Determining Insect Numbers

Summary

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An automated egg-mass counter has been developed and the current prototype is being tested now. Egg mass sampling systems seem to be adequate, but the trend is to replace them with overwintering larval sampling. The latter appears to be more reliable and cheaper.

Sampling of overwintering larvae needs to be refined to allow for more precise population estimates, especially when measuring the effect of direct or indirect treatments. A new data base is needed to establish decision lines in sequential sampling systems for species of spruce. An automated counter of second-instar larvae would greatly enhance the efficiency of overwintering larval sampling. Randomization of samples within stands is still a theoretical problem, but more important may be the problem of annual fluctuation of hibernation sites within a tree. Research into the latter might explain the occasional inaccurate prediction that is made. Also, new data are required to redefine decision lines of sequential sampling systems in young stands, in thinned stands, or in stands receiving other types of silvicultural treatments.

A new thought was expressed that a better sample unit should be found for sampling budworm numbers, such as dry weight of total foliage or dry weight of new foliage. This research could take advantage of known relationships between foliage present and easily measured tree parameters.

Researchers on budworm pheromone sampling were united in foreseeing a continued need to calibrate existing pheromone traps to enable better correlation of trap catch to numbers of a given life stage of the budworm present per tree, per stand, or per unit area. The most urgent need is to get user involvement, which should lead to user feedback and to "a better...trap."

Discussion Group B —
Quantifying Impacts on
Forest Growth and Yield

The Impact of the Spruce Budworm on the Growth Response of Trees in the Spruce-Fir Forests of the Eastern United States

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The defoliation of the spruce-fir forest in the northeastern United States by the spruce budworm (*Choristoneura fumiferana* (Clem.)) has caused forest managers concern about the reduction in growth of trees. Continued defoliation of the current foliage alters growth and may kill the tree as the reduced foliage in the current age class enters the older age classes. The severity and length of attack reduce the growth of the spruces but may kill balsam fir, eastern hemlock, and red spruce.

Different intensities of defoliation and different defoliation histories place balsam fir trees in spruce-fir stands under different intensities of growth stress. Increasing defoliation from 20 to 70 percent over 6 years reduced annual volume growth by 35 to 50 percent (Kleinschmidt et al. 1980; Solomon 1983). Severe defoliation, from 85 to 90 percent of current foliage on balsam fir, reduced the annual volume growth by 45 to 50 percent over 7 years (Solomon 1983). Continued annual defoliation of the current foliage alters the amount of foliage that remains on the tree to enter the older age classes. Volume growth of the bole is reduced as defoliation continues (Solomon 1985). Radial increments are reduced first in the upper bole after 1 or 2 years of defoliation and over the whole bole as the remaining foliage enters the third and fourth age classes (Figure 1). As trees are protected, or as the amount of defoliation decreases, the growth along the bole increases. One-time protection of full-grown, dominant balsam firs increases the radial increment in the upper bole, but has little effect on the growth decline at breast height. With moderate protection of full-grown codominant trees, the decline in bole-volume growth can be reduced and the rate of growth maintained. With intensive protection of young, dominant balsam fir, not only can the decline in bole-volume growth be reduced, but it can also be restored to previous rates. The growth response to continued protection happens first in the upper bole and then in the lower bole, as the increased foliage remaining survives into the older age classes.

Severe, continued defoliation eventually kills the tree. Balsam fir has about twice as much volume loss to the growing stock as spruce (Brann et al. 1983; Witter et al. 1985). Mortality decreases as the mean stand diameter increases, primarily because of the large component of fir with smaller mean stand diameters. Also, mortality increases as the severity and length of attack continue. Both the amount of balsam fir in the stand and the intensity and duration of attack cause mortality to differ from stand to stand. Certainly the amount of mortality and the possibility of salvaging or harvesting dead or heavily affected trees are of primary concern to the forest manager. Some of the major criteria for predicting salvage yields from spruce-fir stands infested by spruce budworm are the amount of host species in accessible areas, market availability, and defoliation history.

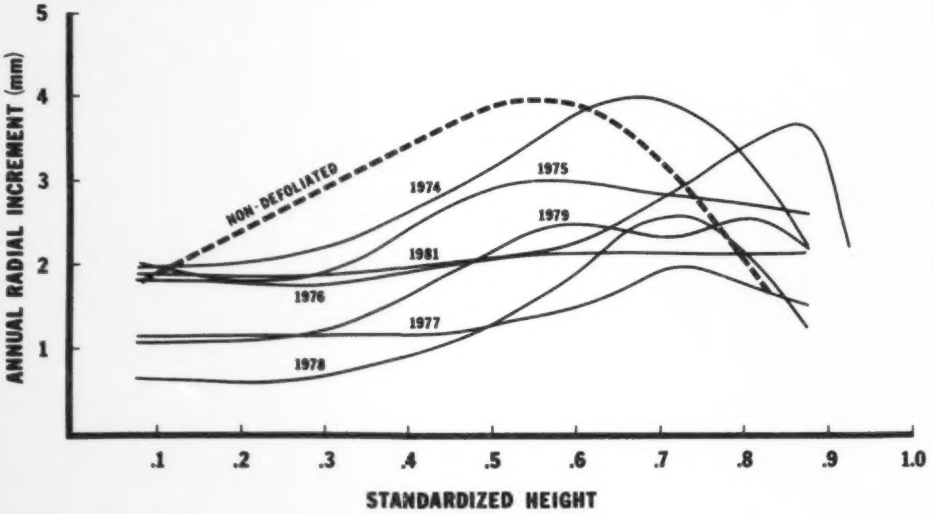

Figure 1. Annual radial increment at standardized heights (height above ground/total tree height) for dominant defoliated and nondefoliated balsam fir trees intensively protected.

Literature Cited

Brann, T.B.; Reams, G.A.; Solomon, D.S. 1983. Spruce budworm growth impact study — 1981 report. CFRU Res. Note II. Univ. Maine Agric. Exp. Stn., Orono, Maine. Misc. Rep. 287.

Kleinschmidt, S.M.; Baskerville, G.L.; Solomon, D.S. 1980. Reduction of volume increment in fir-spruce stands due to defoliation by spruce budworm. Faculty of Forestry, Univ. New Brunswick, Fredericton, N.B. 37 p.

Solomon, D.S. 1983. Changes in growth of spruce-fir stands in the Northeast under varying levels of attack by the spruce budworm. Pages 93-96 *in* J.F. Bell and T. Atterbury, eds. Proc. Renewable resource inventories for monitoring changes and trends. Oreg. State Univ. Press. Corvallis, Oreg.

Solomon, D.S. 1985. Growth responses of balsam fir defoliated by spruce budworm. Pages 105-111 *in* D. Schmidt, ed. Spruce-fir management and spruce budworm. Proc. Soc. Am. For. Region VI Tech. Conf., Burlington, Vt., U.S. Dep. Agric., For. Serv., Northeast For. Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-99. 217 p.

Witter, J.A.; Lynch, A.M.; Mog, T.P.; Montgomery, B.A. 1985. Assessing spruce budworm damage in Michigan's upper peninsula, 1978–1983: a case study. Pages 41-53 *in* D. Schmidt, ed. Spruce-fir management and spruce budworm. Proc. Soc. Am. For. Region VI Tech. Conf., Burlington, Vt. U.S. Dep. Agric., For. Serv., Northeast For. Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-99. 217 p.

Discussion Group B —
Quantifying Impacts on
Forest Growth and Yield

Quantifying Effects of Spruce Budworm Damage in Eastern Canada

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The spruce budworm (*Choristoneura fumiferana* (Clem.)) is currently the most destructive forest insect in eastern Canada. Defoliation of host trees results in loss of volume increment, decreased vigor in roots and rootlets, the inability of the tree to initiate the development of flowers and produce seed, reduced tree size because of top-killing, increased wood decay, tree deformities, and ultimately, tree mortality. Budworm outbreaks affect the species composition of the forest, the age-class distribution, and volume production, which can affect forest-management decisions that rely on the ability to predict volume production in the future. Losses differ between stands, regions, and outbreaks, and predicting total expected mortality poses problems.

The current budworm outbreak started in the late 1960s in northeastern Ontario, western Quebec, central New Brunswick, and Maine (Kettela 1983). The average annual tree mortality caused by the budworm from 1977 to 1981 was estimated to be more than 38 million m^3 (1.34 billion ft^3), an amount equivalent to about two-thirds of the annual harvest and about one-half of the annual allowable cut of softwoods in eastern Canada (Sterner and Davidson 1982). By 1983, tree mortality occurred within 26 million hectares (64,246,000 acres) of susceptible forests (Table 1). The amount of mortality resulting from budworm outbreaks is a function of severity and duration of defoliation, the species and age of trees attacked, and stand characteristics, such as age-class distribution, species composition, spacing, and site (MacLean 1980).

Quantifying budworm impact is necessary to forecast yields and establish priority and timing for stand-management strategies (harvesting, silvicultural treatments, and protection). Data on effects on individual trees are collected from semipermanent or permanent sample plots. Although experimental design, plot layout, and sampling intensity may differ, most studies include annual assessment of defoliation and insect numbers, followed by determination of volume or radial increment loss (Archambault 1983; Bryant and Raske 1976; Piene et al. 1981). Estimates of volume of dead host material are derived from aerial surveys, ground surveys, or both (Dorais and Kettela 1982). Accuracy

Table 1
The effect of the spruce budworm in eastern Canada in 1983 with an estimate of tree mortality since 1977

Province	Area of moderate to severe defoliation (000 ha)	Area of moderate to severe defoliation (000 acres)	Area of tree mortality (000 ha)	Area of tree mortality (000 acres)	Average annual[1] mortality volume 1977–81 (million m^3)	Average annual[1] mortality volume 1977–81 (million ft^3)	Mortality volume 1982 (million m^3)	Mortality volume 1982 (million ft^3)	Mortality volume 1983 (million m^3)	Mortality volume 1983 (million ft^3)
Newfoundland	*68.0*	*168.0*	*458*	*1,132*	*3.7*	*130.7*	*2.4*	*84.7*	*2.6*	*91.8*
Prince Edward Island	*22.2*	*54.8*	*30*	*74*	—[2]	—[2]	—[2]	—[2]	*0.1*	*3.5*
Nova Scotia	*294.2*	*727.0*	*800*	*1,977*	*3.1*	*109.5*	*4.4*	*155.4*	*1.9*	*67.0*
New Brunswick[3]	*2 028.0*	*5,011.0*	*1 000*	*2,471*	*4.6*	*162.4*	*5.8*	*204.8*	*3.9*	*137.7*
Quebec	*12 265.6*	*30,308.3*	*12 085*	*29,862*	*14.8*	*522.7*	—[2]	—[2]	—[2]/	—[2]/
Ontario	*9 040.0*	*22,337.8*	*12 120*	*29,948*	*11.6*	*409.6*	*14.6*	*515.6*	—[2]/	—[2]/
	23 718.0	*58,606.9*	*26 493*	*65,464*	*37.8*	*1,334.9*	*27.2*	*960.5*	*8.5*	*300.0*

[1] Figures taken from Depletion Estimates submitted by Forest Insect and Disease Survey in each region to the Director, Forest Insect and Disease Survey, Ottawa, Ontario, 1981.

[2] Data not available.

[3] Volume and area data were obtained from New Brunswick Forest Inventory Data, 1981, and some of data used in estimating damage were obtained from Clowater, W.G.; Andrews, P.W. 1981. An assessment of damage caused by the spruce budworm on spruce and balsam fir trees in New Brunswick. For. Manage. Branch, Dep. Nat. Res., Fredericton, N.B. 23 p.

and precision of impact estimates depend on plot size and sampling intensity (MacLean and Ostaff 1983).

When extensive areas of tree mortality or severe cumulative defoliation occur, estimates of damage can be made using remote-sensing techniques, e.g., small-scale (1:60,000) color-infrared aerial photography, single date Landsat data, multidate Landsat data with image enhancement, and airborne multispectral scanner data.

Faced with potential wood shortages, many regions are trying to protect high-value, managed stands as well as remaining old-growth timber stocks. The development of appropriate stand-management strategies may depend, in part, on the ability to quantify damage caused by insects and diseases. Thus, developing improved methods to quantify pest losses is essential.

Literature Cited

Archambault, L. 1983. Impact of defoliation caused by the spruce budworm on volume growth in three fir stands. Can. For. Serv., Ottawa, Ont. Res. Notes 3:17-19.

Bryant, G.D.; Raske, A.G. 1976. Impact of the spruce budworm on some major forest types in Newfoundland. I. Plot establishment and methods. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. File Rep. Study 15-6 (76-77A).

Dorais, L.; Kettela, E.G. 1982. A review of entomological survey and assessment techniques used in regional spruce budworm, *Choristoneura fumiferana* (Clem.), surveys and in assessment of operational spray programs. A report of the Committee for Standardization of Survey and Assessment Techniques. Eastern Spruce Budworm Council, Ministere de l'énergie et des Resources, Quebec, Que. 43 p.

Kettela, E.G. 1983. A cartographic history of spruce budworm defoliation 1967 to 1981 in eastern North America. Can. For. Serv., Ottawa, Ont. Inf. Rep. DPC-X-14.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56:213-221.

MacLean, D.A.; Ostaff, D.P. 1983. Sample size-precision relationships for use in estimated stand characteristics and spruce budworm-caused tree mortality. Can. J. For. Res. 13:548-555.

Piene, J.; MacLean, D.A.; Wall, R.E. 1981. Effects of spruce budworm caused defoliation on the growth of balsam fir: experimental design and methodology. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-128.

Sterner, T.E.; Davidson, A.G. 1982. Forest insect and disease conditions in Canada. 1981. For. Insect and Dis. Surv., Can. For. Serv., Ottawa, Ont. 46 p.

Discussion Group B —
Quantifying Impacts on
Forest Growth and Yield

Quantifying Impacts on Forest Growth and Yield — Western United States

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The interaction between the western spruce budworm and forests in the western United States is complex. Some areas suffer chronic defoliation, many areas have periodic outbreaks, and still other areas are rarely affected even though large, contiguous areas of host type exist. Ecology of host species is highly variable. Silvicultural opportunities to reduce damage range from poor, where only host species regenerate, to excellent, where nonhost species can provide stocking. Researchers in the West have concentrated on quantifying the effects of the western spruce budworm on trees and stands so that alternative management plans can be compared.

Large trees are affected by loss of height and diameter growth, top-kill, reduced crown ratio, forked tops, loss of cones, poor form, deformities, and mortality. Losses depend on the intensity and duration of defoliation, but they are most substantial when the stand is mostly or exclusively host species. Nonhost species in mixed stands can increase growth rates during periods of budworm outbreak and the western spruce budworm sometimes acts as a crude but effective thinning agent.

Studies of the effect of budworm on tree growth have been conducted throughout the western United States. Nichols[1] studied height and diameter growth of Douglas-fir and grand fir in north-central Washington. Beveridge and Cahill (1984) reported on height, radial, and volume losses in mixed stands in central Idaho, while Mika[2] reported on a similar study in north-central Washington. Hinckley et al.[3] worked with Douglas-fir in Washington, and Swetnam[4] has shown techniques for quantifying radial-growth losses.

Defoliation to host trees of seedling-to-sapling size is heaviest when overstory trees are nearby, such as in multistoried stands, partial cuttings, or the edges of clearcuts that border adjacent, uncut timber. The overstory trees need not be host species. Small trees growing in even-aged silvicultural systems are rarely defoliated. When small trees are defoliated, however, height-growth loss is significant.[5] Regeneration-size trees also suffer top-kill, loss of terminals, reduced crown ratio, multiple tops, poor form, and mortality. Wounds can serve as entry courts for decay fungi. Wissenbach (1982) concluded that the western spruce budworm reach sapling-sized western larch by larval dispersal.

The western spruce budworm also affects the process of regeneration establishment. Seed-bearing trees suffer top-kill (especially important for true firs), cone destruction, mortality, and reduced tree vigor, which reduces the frequency and viability of seed crops. Seedlings are often killed before final overstory removal, or if growing in uneven-aged stands. Defoliation of regeneration in partial cuttings makes it difficult for trees to adjust to overstory removal.

The western spruce budworm does not substantially reduce the probability that a small plot will be stocked with acceptable seedlings, except for some of the drier sites.[6,7] The probability of host species is reduced, however, thereby changing seedling density and species composition in the new stand.

Habitat types — a land-classification system based on potential climax vegetation (Daubenmire and Daubenmire 1968) — provide a logical framework within which to study the western spruce budworm. For example, within a habitat type, the budworm shows differential feeding preference among host species. Thus, habitat types are useful in predicting the susceptibility and vulnerability of stands to attack and are used to hazard-rate stands (Wulf and Carlson, in press).[8] Silvicultural recommendations, such as those by Carlson et al. (1985), rely on habitat types.

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[1] Nichols, T. 1984. Western spruce budworm impact model calibrations. Final report to CANUSA-West. On file at: U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR.

[2] Mika, P.G. 1984. Western spruce budworm impact assessment: hazard model validation and vulnerability model development. Final report to CANUSA-West. On file at: U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 123 p.

[3] Hinckley, T.M.; van der Wal, D.W.; Klein, E.L.; Chapman, R.J.; Schulte, P.J. 1983. Relationship between sapwood basal area/dbh, defoliation, and foliage biomass/growth of *Pseudotsuga menziesii*. Final report to CANUSA-West. On file at: U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 177 p.

[4] Swetnam, T.W. 1983. Radial growth assessment of western spruce budworm infected Douglas-fir trees on the Carson National Forest, New Mexico. Univ. Ariz. report. 28 p.

[5] Ferguson, D.E.; Stage, A.R. 1982. Impact of defoliation by spruce budworm on growth and development of young timber stands in Idaho. Progress report to CANUSA-West. On file at: U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 32 p.

[6] Carlson, C.E.; Theroux, L.J.; McCaughey, W.W. 1982. The influence of silvicultural practices on the susceptibility and vulnerability of northern Rocky Mountain forests to the western spruce budworm. Progress report to CANUSA-West. On file at: U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 55 p.

[7] Ferguson, D.E.; Stage, A.R. 1982. The effects of spruce budworm on regeneration success in Idaho's forest ecosystems. Progress report to CANUSA-West. On file at: U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 32 p.

How can the complex interaction of the western spruce budworm and stand dynamics be processed, examined, and displayed in a meaningful way? Western foresters can use the CANUSA-West Decision Support System.[9] This model assimilates much of the known impacts to forest growth and yield caused by the western spruce budworm. A tree-growth component of the model interacts with a component predicting insect dynamics. Variables used in the Decision Support System are compatible with present inventory methods. Future work on the western spruce budworm can be incorporated as these data become available.

We still need to find a way to quantify the amount of foliage remaining after budworm feeding because this foliage produces photosynthates. We also need to know the efficiency of different age classes of foliage and how efficiency and needle retention change as a result of budworm feeding.

Literature Cited

Beveridge, R.L.: Cahill, D.B. 1984. Western spruce budworm feeding effects on conifers located on the Boise and Payette National Forests. U.S. Dep. Agric., For. Serv., For. Pest Manage., Intermt. Reg., Boise, ID. Rep. 84-7. 32 p.

Carlson, C.E.; Schmidt, W.C.; Fellin, D.G.; Wulf, N.W. 1985. Silvicultural approaches to western spruce budworm management in the northern U.S. Rocky Mountains. Pages 281-300 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20 Sept. 1984. Bangor, ME. Can. For. Serv., Ottawa, Ont.

Daubenmire, R.; Daubenmire, J.B. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Stn., Wash. State Univ., Pullman, Wash. Tech. Bull. 60. 104 p.

Wissenbach, M.J. 1982. Quantitative and temporal analysis of western spruce budworm damage to western larch. Univ. Idaho, Moscow, ID. M.S.. thesis. 71 p.

Wulf, N.W.; Carlson, C.E. (In press). Rating stand hazard to western spruce budworm. Chapter 6 *in* M.H. Brookes, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech. eds. Managing trees and stands susceptible to western spruce budworm. U.S. Dep. Agric., Washington, D.C. Tech. Bull. 1696.

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[8] Stoszek, K.J.; Mika, P.G. 1983. The relationships of western spruce budworm outbreaks to site/stand attributes, development and management history: model completion and comparison. Final report to CANUSA-West. On file at: U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 70 p.

[9] Colbert, J.J.; Crookston, N.L.; Kemp, W.P.; Srivastava, N. 1981. Description of the combined Prognosis/western spruce budworm model version 3.0. CANUSA-West. On file at: U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. 26 p.

Discussion Group B —
Quantifying Impacts on
Forest Growth and Yield

Factors Affecting Loss in Radial Growth of Douglas-fir Caused by Western Spruce Budworm Defoliation

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The effect of defoliation on radial growth typically consists of a progressive narrowing of the radial-growth layer laid down each year by the tree (Figure 1). The decline lags 1 to 2 years behind the onset of defoliation. Recovery also begins 1 to 2 years after budworm feeding stops. Recovery to preinfestation growth rates takes a period about equal to the defoliation period. The total number of rings of below-normal growth resulting from an infestation has been termed the "loss period" (Alfaro et al. 1982). The following summary of important factors affecting the magnitude of loss in radial growth is based on our recent analysis of survey data, as well as on simulation studies.

Budworm infestations in British Columbia have lasted from 1 to 15 years and extended over large areas (226 000 ha [558,446 acres] in 1976). Infestations start as localized centers and spread in successive years to adjacent stands (Shepherd 1977); thus, the duration of the defoliation is not uniform throughout the infested area. The epicenter sustains the longest duration and, therefore, the highest losses. Marginal areas sustain shorter durations and lower losses. Defoliation intensity and, consequently, radial losses differ considerably from tree to tree within a stand. Uneven larval distribution in the stand and differences in host phenology determine the variation in defoliation intensity. The relation of expected radial loss to the duration and intensity of defoliation is given in Figure 2, which is based on simulation studies representing the defoliation conditions and tree-growth rates observed in the 1969–1975 infestation in the Pemberton Valley, British Columbia.

Radial losses, relative to the preinfestation growth rates, are greatest on fast-growing trees, such as young, dominant trees on good sites. Trees suffering from competition, growing on poor sites, or old age do not show a marked defoliation effect on their already reduced growth rates. These trees may be more prone to mortality, however.

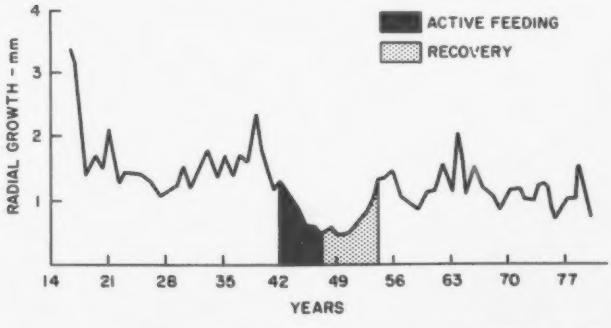

Figure 1. Effects of severe defoliation on a tree from Vesey Lake, British Columbia.

Growth-loss estimates are obtained by comparing the period of reduced growth with normal or "control" growth; therefore, choosing the control is critical. Thomson and Van Sickle (1980) and Carlson and McCaughey (1982) compared growth during the loss period with growth before and after — a "within-tree" method, which assumes that growth returns to "normal" after the infestation. Postinfestation growth for a particular tree may be higher or lower than expected, however. For example, if mortality occurs in the surrounding trees, then a release effect may increase growth — as has been shown for other insects (Wickman 1980).

Losses can also be derived by comparing reduced growth to growth of a nondefoliated host or to the growth of nonhost trees in the area — a "between-tree" method. Budworm infestations are often so extensive that a nondefoliated host can only be found at considerable distance from the defoliated trees and have different, noncomparable growth regimes. Host trees escaping defoliation and nonhost trees within a defoliated stand are usually not satisfactory as controls because they often show higher than expected growth owing to the release effect caused by defoliation of neighboring trees. The problems associated with both methods may be reduced by careful selection of the trees to be studied.

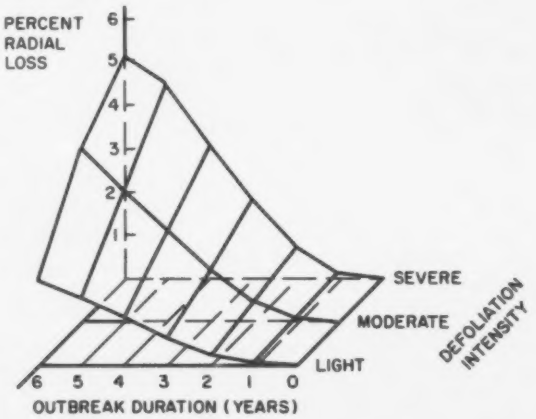

Figure 2. Radial growth loss by rotation age (100 years) after simulating infestations of varying duration and intensity on a 55-year-old tree.

Whether losses should be measured at breast height or in the upper stem has been discussed extensively (see MacLean 1981). Several reports indicate that because rings are wider within the crown than in the lower stem, ring-width reduction is greater in the crown. But we have also noticed that growth recovery occurs sooner and is more vigorous in the upper stem, thereby compensating for the earlier, steeper decline. Thus, radial and particularly basal-area losses, calculated for the entire loss period, were only slightly higher in the upper stem than at breast height. We also found significant correlation and developed regression equations that related the loss at breast height for a given year (i.e., based on individual rings) to the losses calculated at various points up the stem in the same year. Once such relations are established for a sample of trees, borings at breast height are sufficient to estimate radial losses at any stem height in the rest of the trees.

Foresters are ultimately interested in volume losses to the whole stand, which requires estimation of the losses in height and mortality by crown class, as well as the diameter losses. Height growth losses in British Columbia Douglas-fir have been described by Shepherd et al. (1977) and Van Sickle et al. (1983). Losses to date can be measured in current stands, but calculation of future losses at rotation age require stand-projection techniques. Loss projection is extremely difficult because the budworm affects the factors that determine changes in stand structure over time, i.e., increasing mortality and reducing crown size and competition. Loss projection is probably the greatest challenge that forest-pest managers are facing today.

Literature Cited

Alfaro, R.I.; Van Sickle, G.A.; Thomson, A.J.; Wegwitz, E. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. Can. J. For. Res. 12:780-787.

Carlson, C.E.; McCaughey, W.W. 1982. Indexing western spruce budworm activity through radial increment analysis. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn., Ogden, UT. Res. Pap INT-291. 10 p.

MacLean, D.A. 1981. Impact of defoliation by spruce budworm populations on radial and volume growth of balsam fir: a review of present knowledge. Mitteilungen der Forstlichen Bundesversuchsanstalt Wien. 142:292-305.

Shepherd, R.F. 1977. A classification of western Canadian defoliating insects by outbreak spread characteristics and habitat restriction. Univ. Minn., Agric. Exp. Stn., Minneapolis, Minn. Tech. Bull. 310. Pages 80-88.

Shepherd, R.; Harris, J.W.E.; Van Sickle, A.; Fiddick, L.; McMullen, L. 1977. Status of western spruce budworm on Douglas-fir in British Columbia. Can. For. Serv., Pac. For. Res. Cent., Victoria, B.C. Pest Rep.

Thomson, A.J.; Van Sickle, G.A. 1980. Estimation of tree growth losses caused by pest activity. Can. J. For. Res. 10:176-182.

Van Sickle, G.A.; Alfaro, R.I.; Thomson, A.J. 1983. Douglas-fir height growth affected by western spruce budworm defoliation. Can. J. For. Res. 13:445-450.

Wickman, B.E. 1980. Increased growth of white fir after a Douglas-fir tussock moth outbreak. J. For. 78:31-33.

Discussion Group B — Quantifying Impacts on Forest Growth and Yield

Growth Loss and Recovery of Balsam Fir from Spruce Budworm Defoliation

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Current harvesting practices in eastern Canada are quickly changing the forest composition to one that increasingly has a higher percentage of young stands. In recent years, large sums of money have been invested in silvicultural practices, such as planting and spacing. Unfortunately, many of these high-investment stands are being defoliated by the spruce budworm (*Choristoneura fumiferana* (Clem.)). This defoliation could have a serious effect on the future wood supply, especially in New Brunswick where a timber deficit is predicted to occur 20 to 30 years from now (Reed and Associates Ltd. 1978). Thus, to be able to make accurate projections of timber supply for management planning, we urgently need information on the impact of defoliation on tree growth in these young high-value stands.

This brief report reviews the effects of defoliation caused by spruce budworm on volume and height growth in stands of balsam fir (*Abies balsamea* (L.) Mill.), based on studies conducted in eastern Canada.

Removal of part of a tree's photosynthetic surface area results in decreased volume growth and, after repeated defoliation for several years,top-kill and eventually mortality may occur. Raske et al. (1982) reported decreases from 47 to 86 percent in volume increment for surviving trees after 3 to 5 years of severe defoliation in semimature balsam fir stands in Newfoundland. In Quebec, average decreases in annual volume growth during 8 years of light-to-severe defoliation in balsam fir stands ranged from 22.5 to 33.2 percent (Archambault 1983). Blais (1964) reported average decreases in ring width at breast height over an 11-year defoliation period of 46 percent for balsam fir, 36 percent for white spruce (*Picea glauca* (Moench) Voss), and 18 percent over a 7-year period for black spruce (*Picea mariana* (Mill.) B.S.P.).

Decreases in height growth may be separated into different categories: reduced growth without leader destruction, leader destruction, top-killing, and reduced growth of a new leader. A combination of the last three types is most common during severe spruce budworm outbreaks. Baskerville and MacLean (1979) reported that height-growth losses of 3 to 4 m (10 to 13 ft) resulted from a severe outbreak in immature balsam fir stands in New Brunswick, and those losses persisted for 20 years after the outbreak.

Accurate information about results of various degrees of defoliation on changes in volume growth in young silviculturally treated stands is important to the forest industry. Therefore a detailed study was started in 1976 in 25- to 30-year-old spaced and unspaced balsam fir stands on the Cape Breton Highlands, Nova Scotia (Piene et al. 1981). Preliminary results from this study have shown that balsam fir is extremely sensitive to defoliation. During the first year of insect feeding on the current year's foliage, a concomitant reduction in volume growth occurred (Piene 1980). Defoliation of current year's foliage, ranging from 60 to 100 percent, reduced annual-volume increment about 20 percent, while losses of two age classes of needles resulted in a decrease of about 50 percent in volume increment (Piene 1980).

This study has also shown that balsam fir has a remarkable ability to recover from a spruce budworm outbreak if satisfactory protection is provided by insecticide application. One plot was completely defoliated of all age classes of needles in 1977, and was subsequently sprayed yearly thereafter from the ground. In 1979, the second year of the refoliation period, the number of shoots produced per centimetre branch length was similar to that produced by adjacent undefoliated trees (Piene and Percy 1984). The rapid increase in number of shoots diminished the third year of the refoliation period, which also was the first year of a significant increase in current annual volume increment (H. Piene, unpublished). Another spaced plot that had undergone nearly complete defoliation of all age classes in 4 years, also showed good recovery rates, after protection with insecticide (H. Piene, unpublished). In comparison, Baskerville and MacLean (1979) reported that only 2 of 10 plots in immature balsam fir stands recovered (no insecticide applied) in volume per hectare to predamage levels 17 years after a spruce budworm outbreak, which collapsed in New Brunswick in 1958.

In summary, balsam fir is extremely sensitive to defoliation, and during the first year of insect feeding on the current year's foliage, a concomitant reduction in volume growth occurs. Light to severe defoliation for up to 10 years reduced volume increment in balsam fir from 22.5 to 86.0 percent. Also balsam fir recovers quickly after several years of defoliation if satisfactory protection is provided by insecticide application. It is recommended that additional detailed studies be initiated in young silviculturally treated stands.

Literature Cited

Archambault, L. 1983. Impact of defoliation caused by the spruce budworm on volume growth in three fir stands. Can. For. Serv., Ottawa, Res. Notes 3:17-19.

Baskerville, G.L.; MacLean, D.A. 1979. Budworm-caused mortality and 20-year recovery in immature balsam fir stands. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-102.

Blais, J.R. 1964. Account of a recent spruce budworm outbreak in the Laurentide park region of Quebec and measures for reducing damage in future outbreaks. For. Chron. 40:313-323.

Piene, H. 1980. Effects of insect defoliation on growth and foliar nutrients of young balsam fir. For. Sci. 26:665-673.

Piene, H.; MacLean, D.A.; Wall, R.E. 1981. Effects of spruce budworm-caused defoliation on the growth of balsam fir: experimental design and methodology. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-128.

Piene, H.; Percy, K.E. 1984. Changes in needle morphology, anatomy, and mineral content during the recovery of protected balsam fir trees initially defoliated by the spruce budworm. Can. J. For. Res. 14:238-245.

Raske, A.G.; Clarke, L.J.; Sutton, W.J. 1982. The status of the spruce budworm in Newfoundland in 1981. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. Inf. Rep. N-X-210.

Reed, F.L.C, and Associates Ltd. 1978. Forest management in Canada. Vol. 1. Can. For. Serv., For. Manage. Inst., Ottawa, Ont. Inf. Rep. FMR-X-102.

Discussion Group B —
Quantifying Impacts on
Forest Growth and Yield

Summary

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The general discussion of panel members centered around the differences between the growth loss of host trees in the west and growth loss and mortality of host trees in the east. Information on growth reduction due to attack by the spruce budworm is needed to validate prediction models because present data primarily came from a few permanent plots. These permanent plots and growth loss studies mostly concentrate on the older stands and not on the younger forest, and do not provide reliable estimates of growth loss. The growth in the upper bole is also ignored because most studies consider the growth at breast height. More data are needed both from individual tree studies and by following permanent plots through time. Collecting data on the growth and eventual mortality provides some basis for future modeling efforts. This can be accomplished by refining the measures of defoliation and relating the remaining foliage to the growth of trees prior, during, and after outbreak.

Additional areas of discussion included the extrapolation of western growth loss information, and the need for caution and concern. Also, succession of species within the stand as mortality increases was discussed. Ongoing studies in the east indicate that the species composition of the residual stand tends toward nonhost trees with a large amount of balsam fir regeneration in the understory.

To continue conducting future research and developing data bases, consideration should be given to:

1. Estimates of the amount of foliage on a tree and its relationship to growth both with and without defoliation.
2. More precision is needed in measurement of height and radial growth. This should also include dieback and eventual recovery.
3. Growth recovery of stands under attack and the influence of spray technology and defoliation history.

Discussion Group C —
Quantifying Impacts on
Other Forest Resources

Modeling Social Impacts of Forest Management

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A review of resource models and a companion user-needs survey (Buhyoff and Daniel 1984) was conducted within the USDA Forest Service. Survey results indicate that the use of computerized forest growth and yield models is intensive, widespread, and increasing. Comparatively, the availability and use of socioeconomic models is far behind. Traditional economic analyses, relating management costs and discounted market returns, are frequently used. Sometimes more elaborate input-output analyses are used to assess more detailed effects on local, regional, or national economics. Explicit models of recreation, aesthetic, or wildlife impacts are hardly ever used. These forest resources typically enter the management decision-making system as after-the-fact, verbally stated recommendations, guidelines, general constraints or "rules of thumb" based on expert judgment. Represented in this form, it is not possible to determine the reliability or validity of assessments of these "other forest resources," nor can they be included with any precision, consistency or force in plan formulation, evaluation, or trade-off analyses.

One goal of the Integrated Pest Impact Assessment System (IPIAS) program is to promote the development of explicit models for assessing social impacts and to incorporate them as strong components of a comprehensive forest management information system. Recreation, tourism, and public perception of scenic beauty were included in the IPIAS development plan from the beginning (USDA Forest Service 1979). Specific models that were developed for the Front Range in Colorado achieved varying levels of success. It was demonstrated, however, that such models can be developed and integrated into a forest management information system. The basic requirements for forest social impact models are clear: quantitative measures of resource quantity and quality must be explicitly linked to measurable (manageable) biophysical characteristics of the forest. For example, a useful model for forest aesthetics must be able to predict changes in scenic beauty with reasonable precision (high, medium, or low is not adequate) given changes in forest variables that are typically available from inventory or stand growth and mortality projections (e.g., trees per acre in various size classes). Then the scenic consequences of alternative forest management actions can be assessed and compared with other benefits and costs.

Several models of forest scenic beauty have been developed and applied in the manner described above. Daniel and associates (Arthur 1977; Brown and Daniel 1984; Daniel et al. 1977, 1981; Schroeder and Daniel 1981) have developed models for predicting public perception of the scenic beauty of southwestern ponderosa pine forests, and Buhyoff and his colleagues (Buhyoff and Leuschner 1978; Buhyoff and Wellman 1980; Buhyoff et al. 1982) have developed models for the scenic beauty of forest vistas in the southeast. The ponderosa pine models relate judgments of public panels of scenic beauty to typical forest mensuration parameters (e.g., trees per acre in various size classes, volume of slash and downed wood, and measures of shrubs and ground cover).

The most recent models (Brown and Daniel 1984) are based on over 1,000 forest sites, each assessed for perceived scenic beauty and intensively inventoried. Multiple regression techniques were used to derive mathematical models relating standardized measures of perceived scenic beauty, the Scenic Beauty Estimate (SBE), (Daniel and Boster 1976) to forest inventory parameters. For example, one model for ponderosa pine stands was:

$$\text{Stand SBE} = 4.35 + 3{,}6079\ \text{PP24PL} + .2788\ \text{PDTOT} - 2.2606\ \text{DWV014}$$

Where:

PP24PL = Number per acre of ponderosa pine greater than 24 inches dbh.

PDTOT = Pounds per acre of herbage (grasses and forbs).

DWV014 = Cubic feet per acre of downed wood 0 to ¼.

This model achieved very good statistical quality (adjusted $R^2 = 0.76$, standard error of estimate = 12.02) and is intuitively reasonable; large trees and lush ground cover are positive scenic elements while downed wood has negative effects.

Applying the scenic beauty model in forest management and planning is straightforward. Standard forest inventories could provide the large pine, ground cover, and downed wood measures for forest stands of interest. Substituting these values into the equation above would yield a scenic beauty estimate for the stand. The effects of alternative management actions would be stimulated by an appropriate growth and mortality model (perhaps with a pest component) to provide projected new values (at various time steps) for the relevant forest feature. The projected values for these features would then be entered into the equation to yield expected scenic beauty values.

Using a similar approach, models have also been developed for recreation (e.g., Walsh and Olienyk 1981) and wildlife (Schamberger 1982). Social impact models of this type are only now being developed and they have not been extensively tested or applied. Thus, as with any model, it is always important to test the accuracy of predictions in each new situation, and, if necessary, to calibrate for local conditions. Whether changes in specific social impacts are important in considering and selecting management alternatives will depend on several factors, including the "visibility" of the area and the nature of its use. In any case, having quantitative assessments and predictions based on explicit verifiable models can substantially enhance the forest manager's ability to include social impacts in formulating and evaluating management plans.

Literature Cited

USDA Forest Service. 1979. Meeting summary: planning and design workshop, Feb. 6-7, 1979, U.S. Dep. Agric., For. Serv., Rocky Mountain Region, Fort Collins, CO. 13 p.

Arthur, L.M. 1977. Predicting scenic beauty of forest environments: some empirical tests. Forest Science 23(2):151-159.

Brown, T.C.; Daniel, T.C. (1984). Modeling forest scenic beauty: concepts and applications. U.S. Dep. Agric., For. Serv., Rocky Mountain For. and Range Exp. Stn, Fort Collins, CO. Res. Pap. RM-256. 35 p.

Buhyoff, G.J.; Leuschner, W.A. 1978. Estimating psychological disutility from damaged forest stands. Forest Science 24(3):424-432.

Buhyoff, G.J.; Wellman, J.D. 1980. The specification of a non-linear psychophysical function for visual landscape dimensions. J. Leisure Research 12(3):257-272.

Buhyoff, G.J.; Wellman, J.D.; Daniel, T.C. 1982. Predicting scenic quality for mountain pine beetle and western spruce budworm damaged forest vistas. Forest Science 28(4):827-838.

Buhyoff, G.J.; Daniel, T.C. 1984. Integrated pest impact assessment system: development and operations coordination. U.S. For. Serv., Coop. Agreement 28-C4-320, FY84 Progress Report, September 1984.

Daniel, T.C.; Boster, R.S. 1976. Measuring landscape esthetics: the scenic beauty method. U.S. Dep. Agric., For. Serv., Rocky Mountain For. and Range Exp. Stn., Fort Collins, CO. Res. Pap. RM-167. 66 p.

Daniel, T.C.; Anderson, L.M.; Schroeder, H.W.; Wheeler, L.W., III 1977. Mapping the scenic beauty of forest landscapes. Leisure Sciences 1:35-53.

Schamberger, M. 1982. Habitat: a rational approach to assessing impacts of land use changes on fish and wildlife. Pages 251-259 *in* The Environmental Professional, Vol 4, 1982.

Schroeder, H.W.; Daniel, T.C. 1981. Progress in predicting the perceived scenic beauty of forest landscapes. Forest Science 27(1):71-80.

Walsh, R.G.; Olienyk, J.P. 1981. Final report — recreation demand effects of mountain pine beetle damage to the quality of forest recreation resources in the Colorado Front Range. U.S. Dep. Agric., For. Serv., Rocky Mountain Region, Fort Collins, CO. 150 p.

Discussion Group C —
Quantifying Impacts on
Other Forest Resources

Forest Management Models: A Review and Users Need Assessment

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The initial development of the Integrated Pest Impact Assessment System (IPIAS) focused on the ponderosa pine (*Pinus ponderosa* Laws) forests of the Front Range in Colorado. In particular, models were developed for predicting biological, economic, recreation, and aesthetic effects of a mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak and of alternative insect-targeted management actions for that area. In the current stage of IPIAS research and development, the same basic integrated management information system structure is being applied to lodgepole pine (*Pinus contorta* Engelm.) forests in the Northwest. This test and extension of IPIAS will require several changes to the specific components of the original system; STAND, PEST, and social impact components developed for Front Range ponderosa pine forests cannot be directly applied to Northwest lodgepole pine forests. Thus, more appropriate model components must be found or developed.

To develop a solid basis for the extension of IPIAS, a comprehensive evaluation is being conducted of currently available models which might be candidates for application in the targeted northwest area (USDA-FS Regions One and Six). At the same time, a survey of model use and user satisfaction/needs at regional, forest and district levels has been initiated (Buhyoff and Daniel 1984). First, models have been identified and evaluative criteria developed, based on intensive personal interviews with individuals in Washington, D.C., in the Forest Research Stations, and in the Region One and Six staffs. Fifty-five individuals, all very familiar with the development and use of models for forest management and planning, were directly contacted in this phase of the evaluation and survey. As a result, 40 separate models or model extensions have been identified and evaluated and 29 models have been entered into a computer data base management system for quick reference and update. Documentation has been obtained for each model and where necessary, individuals who can clarify their use have been contacted.

The 29 models were deemed to have generalized applicability to Regions One or Six or to lodgepole pine, or to be potentially useful for assessing impacts as the result of mountain pine beetle infestations, or for making predictions regarding the behavior of such infestations. The 11 other models were comprehensively evaluated, but not included in the data base as their

Table 1
Models evaluated for IPIAS extension

A. **Growth and Yield**
- *PROGNOSIS*
- *TRAS*
- *FREP/STEMS*
- *TWIGS*
- *TRIM*
- *ECOSIM*
- *GROW*
- *DFSIM*
- *INDIDS*
- *TREES*
- *R2GROW*
- *RMYLD*

B. **Insect/Pest**
- *PROGNOSIS extensions:*
- *Western Spruce Budworm*
- *Douglas-Fir Tussock Moth*
- *Dwarf Mistletoe*
- *Mountain Pine Beetle*
- *TREE LOSS FROM MOUNTAIN PINE BEETLE INFESTATIONS*
- *INDIDS*
- *LP-DM-VOL*

C. **Economic Efficiency**
- *CHEAPO*
- *FORESTRY INVESTMENT ANALYSIS*
- *TRIM*
- *DPDFSIM*
- *LP-DM-VOL*

D. **Harvest Scheduling**
- *TREES*
- *PROGNOSIS extension: EVENT MONITOR*

E. **Wildlife**
- *ECOSIM*
- *PROGNOSIS extension: COVER*

F. **Hydrology**
- *ECOSIM*

G. **Economic-Input/Output**
- *IMPLAN*
- *MICRO I/O*

H. **Debris**
- *DEBMOD*

I. **Comprehensive Simulation**
- *ECOSIM*

applicability to IPIAS was considered minimal or nonexistent. In addition, 32 more trend prediction, management simulation, hazard rating, and growth models specific to southern pine beetle were evaluated and assessed as to their potential applicability to IPIAS. These models were not directly applicable to the development of IPIAS in Regions One and Six and were not included in the model data base, but several of the models and model concepts represented have served as useful guides for the IPIAS effort.

The 29 models now in the data base are categorized by prediction or analysis type and are presented in Table 1. Some models appear under more than one category because they perform more than one type of prediction or analyses.

Note that no range, recreation use, or visual quality models are listed. Although methods exist for developing such models, no specific models, either in use or under development, were identified by the survey. Although the wildlife category displays two models that can aid wildlife impact predictions, one is specifically incorporated in the ECOSIM model itself and the other (PROGNOSIS, COVER extension) makes projections of changes in shrubs and canopy that can potentially be used as input for wildlife population models. In fact, from our research, it seems that "rules of thumb" are more prevalent than are mathematical formulations for making predictions of changes in wildlife levels.

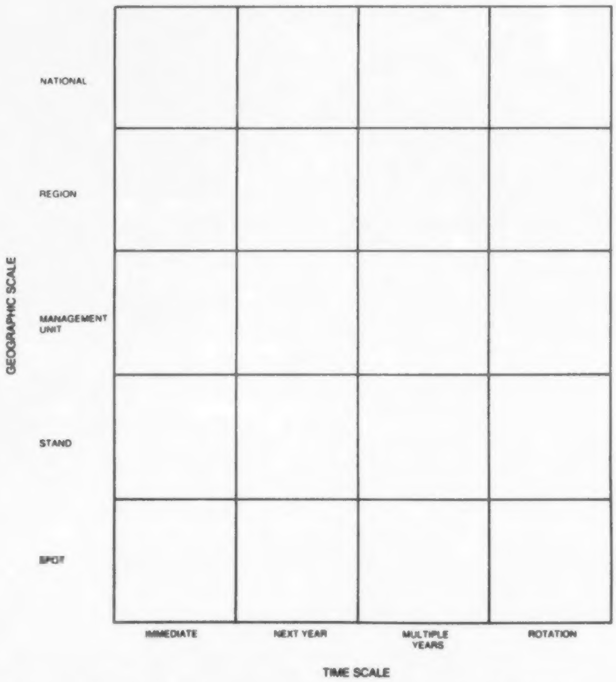

Figure 1. Time and geographic scale matrix incorporating model name and predictive information appropriate to integrated pest impact assessment systems.

At this stage of the IPIAS program it is very difficult to further categorize the models which have been inventoried. Further evaluation of these models for the IPIAS system requires that the geographic area and time frame for the predictions be specified. The Integrated Pest Management Program for Southern Pine Beetle (Leuschner 1970 and 1984; Mason 1984) categorized models within a matrix defined by the interaction of time and area. This matrix (Figure 1) provides not only a means of categorizing models, but also a framework for making decisions about what an integrated impact system *should include*. IPIAS might include the entire matrix, some subset of contiguous cells or be restricted to a single cell, depending upon the needs and wishes of potential *users* of the system. One goal of the user needs survey is to help resolve such issues, and discussion of the geographic and time scale question will be a major agenda item for the IPIAS Steering Committee consisting of model users and developers.

Literature Cited

Buhyoff, G.J.; Daniel, T.C. 1984. Integrated pest impact assessment system: development and operations coordination. U.S. Dep. Agric., For. Serv., Coop. Agreement 28-C4-320, FY 84 Progress Report, Sept. 1984.

Leuschner, W.A. 1979. Impact analysis, interpretation, and modeling. Pages 50-53 *in* Waters, W.E., ed. Current topics in forest entomology; selected papers from the XVth International Congress of Entomology. U.S. Dep. Agric., For. Serv., U.S. Government Printing Office, Washington, D.C. Gen. Tech. Rep. WO-8.

Leuschner, W.A. 1984. Introduction to forest resource management. John Wiley and Sons: New York. 298 pp.

Mason, G.N. 1984 (Revised June). Southern pine beetle predictions handbook. U.S. Dep. Agric., For. Serv., Integrated Pest Management RD&A Program, Southern Region, Atlanta, GA.

Discussion Group C —
Quantifying Impacts on
Other Forest Resources

Integrating Social Impacts Assessment into Forest Management and Planning

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A discussion of techniques for assessing impacts of management on "other forest resources" is immediately hampered by the lack of clear definition of terms. "Other forest resources" does not specify the area of concern sufficiently to allow articulation of the relevant issues or development of a systematic approach to their resolution. Before proceeding, it is important to clearly define what is meant by "other forest resources." For our purposes, we will focus upon what are frequently referred to as *Social Impacts*, as those impacts of forest management actions that affect the quality of the human environment. This approach is consistent with environmental legislation (e.g., NEPA, NFMA, and RPA) and would specifically include aesthetic, wildlife, recreation, and wilderness resources.

Current approaches to the assessment of social impacts tend to be more qualitative than quantitative and to rely on expert judgment rather than explicit analytical systems. As a result, it has been difficult to integrate these concerns with more traditional biological and economic factors in the formulation and evaluation of forest management options. Resource managers have recognized the need for more efficient and more effective methods for assessing social impacts, and for better integrating these impacts into the management and decision-making process.

A number of projects (e.g., Buhyoff and Daniel 1984; Rykiel et al. 1984; Turnbow et al. 1984; and Schomberger 1982) have been attempting to address this need. A 5-year research and development project (USDA Forest Service 1983) is currently underway to develop a computer-assisted forest management information system that links together: 1) biological (including forest growth and mortality, yield, and pest effects); 2) economic (stumpage values, management costs, and local and regional economic effects); and 3) social impact (recreation, scenic beauty, and wildlife) components. The Integrated Pest Impact Assessment System (IPIAS) (Daniel et al. 1983), as the name implies, consists of a linked set of models, data bases, and computer programs developed in the context of pest management concerns, specifically mountain pine beetle (*Dendroctonus ponderosae* Hopkins). IPIAS provides information assimilation and presentation rather than attempting to be an optimization or decision-making system. Because of its modular design and basis on vegetation-linked characteristics, IPIAS can be used to address a wide range of forest management problems.

Implementation of an IPIAS-type system within current forest management and planning procedures could take a form similar to that in Figure 1. The starting point is always an inventory of relevant forest resources. The inventory must be complete enough to operate the STAND model. In a typical IPIAS application, the timber staff and forest silviculturalist would run the STAND model, providing the needed parameters and formulating appropriate harvest, thinning, and pest management activities. Pest management specialists would provide up-to-date infestation or damage inventories and other parameters (e.g., attack ratios for insects) needed to integrate the PEST model with the STAND model. Output from the STAND model would drive a set of resource models, each operated and interpreted by the appropriate planning or management specialist. For each modeled management alternative, resource specialists would provide their evaluation and recommendations, supported by the related model projections of location, timing, and magnitude of predicted effects. Mathematical stand growth and economic models are already routinely used and of great value to timber specialists and economists. Recreation, wildlife, and scenic value models are not generally available at this time, but there are some promising efforts underway. When developed and integrated into a comprehensive information system, such models can enhance the precision, reliability, and usefulness of social impact variables in the forest planning and decision-making process.

The 5-year research and development project (USDA Forest Service 1983) charts a course of action to strengthen the current version of IPIAS. Some of the major areas of development are: 1) survey and evaluate user needs; 2) identify appropriate linkage needs between various resource models: wildlife, fire, scenic beauty, recreation, etc.; 3) develop specifications and model contagion phenomenon (risk rating or hazard rating) relative to mountain pine beetle effects in a large contiguous forest type, e.g., lodgepole pine (*Pinus contorta* Engelm.) within a major drainage.

IPIAS is not intended to make decisions for the resource manager; however, it can give him a multidimensional display of the various trade-off interactions expressed in either relative values (e.g., scenic beauty quotients and recreation use days) or various economic parameters (stumpage value, tourist expenditures). The key point for the resource manager to be aware of is that all these impacts cannot be displayed as a simple total or are they necessarily all negative impacts. We can give the manager the information to help him make a decision. We cannot tell him how to weigh the various trade-offs in making his final decision.

Literature Cited

U.S. Fish and Wildlife Service 1983. Final report to USDA Forest Service, Forest Pest Management/ Methods Application Group on a Pest Impact Assessment System Workshop. Milliken, CO, February 13-18, 1983.

Buhyoff, G.J.; Daniel, T.C. 1984. Integrated pest impact assessment system: development and operations coordination. U.S. Dep. Agric., For. Serv., Coop. Agreement 28-C4-320, FY84 Progress Report, September 1984.

Daniel, T.C.; White, W.B.; Hunter, D.O. 1983. Integrated pest impact assessment system: an interface to a forest management information system. U.S. Dep. Agric., For. Serv., Forest Pest Management Methods Application Group, Fort Collins, CO. Rep. No. 84-2, 22 p.

Rykiel, E.J.; Saunders, M.C.; Wagner, T.L.; Loh, D.K.; Turnbow, R.H.; Hu, L.C.; Pulley, P.E.; Coulson, R.N. 1984. Computer-aided decision-making and information accessing in pest management systems, with emphasis on the southern pine beetle (Coleoptera: Scolytidae). Texas A&M University, College Station, TX. 34 p.

Schamberger, M. 1982. Habitat: a rational approach to assessing impacts of land use changes on fish and wildlife. Pages 251-259 *in* The Environmental Professional, Vol. 4, 1982.

Turnbow, R.H. Jr.; Hu, L.C.; Rykiel, E.J.; Coulson, R.N.; Loh, D. 1983. Procedural guide for FERRET, the question analysis routine of the decision support system for southern pine beetle management. Texas Agricultural Experiment Station, College Station, TX. 21 p.

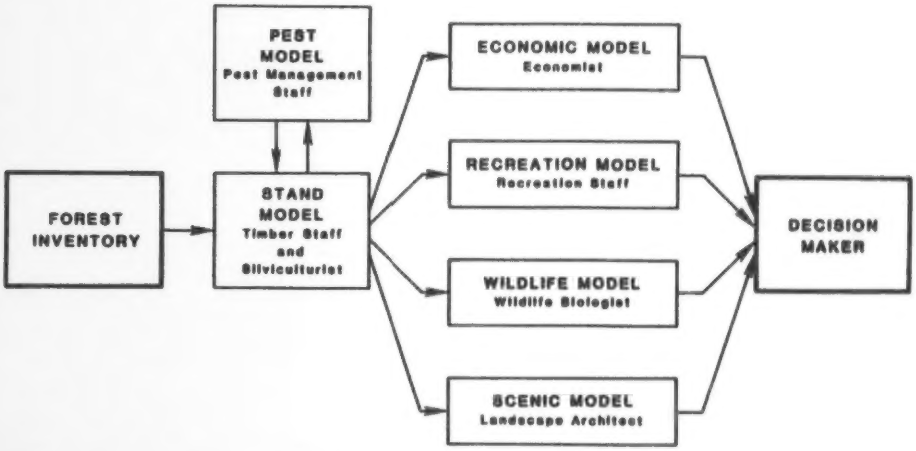

Figure 1. Schematic outline of IPIAS as implemented within a general forest planning framework.

Discussion Group C —
Quantifying Impacts on
Other Forest Resources

Summary

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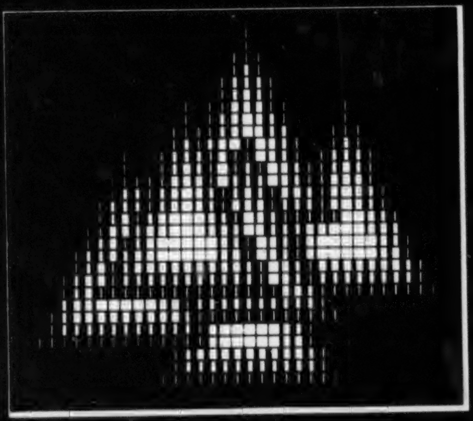
There are several indications, including the proceedings of this symposium, that quantitative computer-implemented models will play an increasingly important role in all aspects of forest planning and management.

Development and integration of these models, and merging them with the other elements of forest management systems will be a major task for research and management. In that context, considerable progress has been made in the measurement and modeling of recreation, wildlife, and aesthetic benefits. The next phase will be to integrate the assessments of impacts on these forest resources into a pest management system.

From information presented at this symposium, it is evident the CANUSA Spruce Budworm Program has made excellent progress in developing some of the major components of a comprehensive impact assessment system. Important biological, silvicultural, and economic relationships have been documented with considerable precision. Although the social impact assessment procedures reviewed were developed in a different context (mountain pine beetle/lodgepole pine), they could be extended and combined with the major budworm biological components to produce a comprehensive management information system. By attention to the linkages among component models, and adding the essential geographic information elements, a valuable operational system could be near at hand.

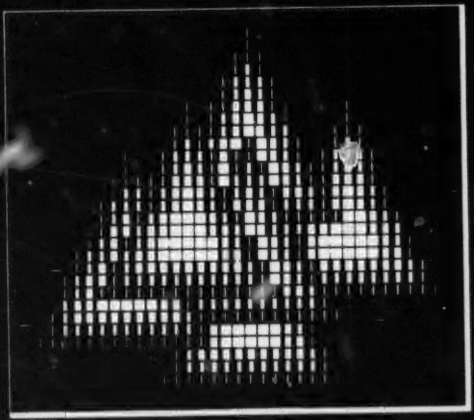
Forest environments are immensely complex and knowledge of how the forest system works and how it is affected by insects and diseases and management actions is continually improving. A 5-year program of research is underway to develop an Integrated Pest Impact Assessment System (IPIAS) for mountain pine beetle in the northwest. Biological, silvicultural, economics, and social impact models are being pulled together to address the management information needs identified by resource managers on the demonstration forest, the Nezperce. This exercise will, no doubt, be a learning experience because there is no point at which a system becomes final.

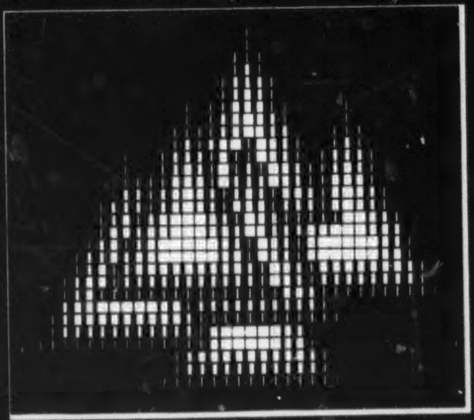
Development of IPIAS will continue, supported by advice on how the overall concept can be kept flexible enough to accommodate other pest applications in the future.



Part III

Tactics and Strategies for Prevention and Suppression of Damage by Spruce Budworm





Potential Silviculture, Harvesting and Salvage Practices in Eastern North America

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Silvicultural techniques have the potential of reducing the vulnerability of spruce-fir stands to spruce budworm damage, thereby alleviating the impact of an infestation. However, silvicultural techniques will not control budworm infestations and should be considered in the context of integrated pest management systems that include other biological techniques and direct control measures. There is a continuing need for the quantification of the reduction in vulnerability to enable a more accurate evaluation of silviculture as a tool. Both even-aged and uneven-aged techniques are applicable, although even-aged systems appear to have the greater advantages.

Silvicultural techniques coupled with forest management offer some potential for reducing susceptibility of spruce-fir forests to budworm attack, over large areas, although recent research in infestation dynamics may alter present approaches.

Implementation of silvicultural techniques in U.S. and Canadian forests is well-documented in a few instances, but up-to-date data are difficult to obtain for some areas. Implementation has not been extensive in those areas where documentation exists.

Les techniques sylvicoles peuvent atténuer la vulnérabilité des peuplements d'épinette et de sapin face à la tordeuse des bourgeons de l'épinette, ce qui, par le fait même, réduit les répercussions d'une infestation. Toutefois, elles ne permettront pas de maîtriser les infestations et elles devraient être envisagées dans le cadre de la lutte intégrée, qui fait appel à d'autres techniques biologiques et à des mesures directes de répression. Le besoin subsiste de mesurer la réduction de la vulnérabilité afin de permettre une évaluation plus exacte de la sylviculture en tant qu'outil de lutte. Les techniques d'aménagement de peuplements équiennes ou non sont utilisables, même si, dans le premier cas, elles semblent plus avantageuses.

Les techniques sylvicoles conjuguées à l'aménagement forestier offrent quelques possibilités de réduire la susceptibilité des forêts d'épinette et de sapin aux attaques de la tordeuse, sur de grandes superficies, même si la recherche récente sur la dynamique des infestations peut modifier les cheminements actuels.

Dans certains cas, nous sommes bien documentés sur l'application des techniques sylvicoles aux États-Unis et au Canada, mais il est difficile d'obtenir des données à jour pour certaines régions. Pour les régions sur lesquelles nous sommes documentés, l'application des techniques n'a pas été extensive.

Introduction

The spruce budworm (*Choristoneura fumiferana* (Clem.)) has been periodically defoliating and damaging forests in eastern North America for hundreds, if not thousands, of years. A total of 11 budworm outbreaks are thought to have occurred in eastern Canada and the United States since 1704 (Blais 1983a). Earlier outbreaks were little more than an entomological curiosity, but as spruce (*Picea* sp.) and balsam fir (*Abies balsamea* (L.) Mill.) began to be extensively used for sawlogs and pulpwood in the 20th century, the budworm threat was regarded more seriously. Damage in uncontrolled outbreaks can be severe: an estimated 200 million and 25-30 million cords (510 million m^3 and 63.75-76.5 million m^3) of fir and spruce were destroyed between 1910-1920 in eastern Canada and Maine, respectively (Swaine and Craighead 1924, McLintock 1955). The consequences of uncontrolled outbreaks are now particularly serious because future timber supply shortfalls are forecast in many regions (e.g., Baskerville 1982; Reed and Associates Ltd. 1978; Sewall Co. 1983).

The occurrence of severe outbreaks of spruce budworm has long been thought to coincide with the development of large tracts of mature balsam fir (Graham 1939; Ghent et al. 1957; Blais, 1973), although recent evidence indicates that outbreaks may actually arise in other forest types (Hardy et al. 1983). Regardless, mature fir forests are most vulnerable in that they suffer the worst damage (tree mortality and growth losses) during outbreaks (MacLean 1980). Early entomologists tended to equate the occurrence of large tracts of balsam fir with improperly regulated cutting practices, forest fires, and natural succession (Graham 1939). There is ample evidence, however, that outbreaks have occurred regularly in the absence of harvesting (Blais 1954), and that stands succeeding these outbreaks often have a high proportion of balsam fir and are ecologically stable in the long term (Baskerville 1975a; MacLean 1984).

The notion that silviculture might alter the patterns leading to the development of these large tracts of mature balsam fir is both logical and attractive. In fact, Pistell and Harshberger (1979) list 14 separate, unique treatment proposals made from 1922 to the present dealing with silviculture and the spruce budworm. Many have roots much earlier than 1922 and most have been repeated often in the budworm literature.

The idea that host management or silviculture has a role in alleviating the impact of budworm outbreaks over the long term is generally accepted. The goal is to create a forest that is less likely to be attacked and damaged while maintaining an economically productive forest (Baskerville 1976). However, the action required is not simple; the very scale in both time and space is overwhelming. Details of necessary operations vary from region to region and site to site, and an intensity of forest management rare to the spruce-fir forest type would be required. It is also clear that silviculture alone will not protect the forest from the budworm. Although essential to any solution to the budworm/forest management problem, silviculture must be applied in the context of an integrated pest management approach that also utilizes more direct measures such as spraying (Baskerville 1976).

Specific silvicultural and management goals recommended in the literature are largely the result of relationships observed among pertinent stand variables and tree mortality. They are working hypotheses rather than proven concepts, and have rarely if ever been tested or quantified. To quote Baskerville (1976) "The status of all the methods (of silviculture) must be considered as conceptual. None have been applied over a sufficient area, over a sufficient time, in the real world to judge their effectiveness. Thus, we are forced to design host management approaches from largely theoretical grounds based on fragmented knowledge and observations of the interaction of the budworm and the forest." For real progress in managing budworm infestations, procedures must be defined in terms of forest type, timing, location, area involved, and their projected results. However, in the absence of quantified relationships between silvicultural actions and reduction in budworm damage, it is logical to proceed on the basis of observed qualitative relationships. Fortunately, most of the silvicultural techniques described, with the possible exception of stand conversion, are only slightly modified from those that would be pursued in an intensive silvicultural program for growth and yield (Blum and MacLean 1984).

Susceptibility and Vulnerability

The interaction between the forest resource and spruce budworm populations are manifested in two related functions — the concepts of *susceptibility* and *vulnerability*. *Susceptibility* of a forest has been defined as the probability that the forest will be attacked by spruce budworm. As such, it is related to those characteristics of the forest that support a given budworm population, as determined by survival and fecundity of the insect. *Vulnerability*, on the other hand, is the probability that damage, in terms of tree growth and mortality, will result from budworm attack. These concepts are interrelated insofar as susceptibility defines the severity of attack and hence the level of damage that is likely to occur (Morris 1958; Mott 1963). However, vulnerability may also be affected in turn by factors other than stand characteristics, such as individual tree condition. The goal of creating a forest that is less likely to be attacked and damaged assumes that forest management and the application of silviculture will result in differing degrees of susceptibility and vulnerability due to changes in tree, stand, or forest characteristics. Changing the forest through silviculture, however, will not control the insect because other factors such as climate or natural enemy complexes also determine budworm survival. These factors can create conditions that enable budworm populations to override whatever limitations are imposed by the forest itself (Blais 1983b; Blum and MacLean 1984).

Long-Term Silvicultural Tactics

Long-term silvicultural tactics are implemented over an entire rotation or longer (ca. 60-80 years), and are designed to reduce the vulnerability of the future forest (Baskerville 1975b). Silvicultural tactics are often mistakenly considered to be forest management in itself. As discussed by Baskerville and Montgomery (1983), forest management consists of 4 elements — scheduling of the harvest or use; distribution of the products of the harvest or use; renewal of the resource; and protection of the resource. Silvicultural tactics deal primarily with the renewal aspects of forest management but in some respects could also be considered an element of forest protection. In the real world, the decision to implement any long-term silvicultural tactic is influenced by a host of forest management constraints such as sustained yield regulation, accessibility, labor, and protection costs, which are in turn constrained by long-term markets and economics. For the sake of this discussion we will consider these constraints minimal, but they should by no means be forgotten.

The Relationship Among Stand Characteristics, Species, and Vulnerability

Most silvicultural tactics have been developed from studies of the relationships among stand characteristics and tree mortality caused by budworm. MacLean (1980; 1982) reviewed the literature dealing with efforts to relate stand characteristics to spruce budworm vulnerability, and the development of vulnerability rating systems. He concluded that of the many attempts to correlate various stand characteristics with vulnerability, only one general association appears to be consistent — mature or overmature stands with a high proportion of balsam fir are the most vulnerable. To quote MacLean (1980) "Beyond this, studies have not successfully related mortality to specific stand characters in a fashion suitable for predictive purposes. This is understandable, because at best, these functions would only predict potential mortality. Intensity and duration of budworm outbreaks are extremely important factors in determining the degree of mortality, and yet, the budworm is influenced by stochastic biological and meteorological factors independent of forest conditions." In spite of this, stand characteristics such as stand structure, stand density, crown exposure, tree vigor and the proportion of nonhost species in the stand have been important variables related to mortality in specific instances, although such relationships have been inconsistent. Recent studies of growth loss of balsam fir due to defoliation (Mott et al. 1957; Kleinschmidt et al. 1980; Solomon 1983) indicate that relationships among stand characteristics and growth loss may be essentially the same as those for mortality, because both are functions of the timing, duration, and intensity of defoliation.

It is evident that manipulating the host forest to alleviate budworm damage is not a very precise science at this point (Blais 1983b). It is also evident that silviculture alone will not "control" the insect, but will alleviate the impact of severe infestations by altering the timing, pattern, and intensity of mortality and growth loss.

Differences in vulnerability among host species are basic to the development of silvicultural recommendations. Balsam fir is the species most vulnerable to damage (Greenbank 1963a). Mortality of fir usually starts about 5 to 7 years after the onset of a severe attack, and mortality in mature or overmature stands can reach 100 percent, especially where fir represents a high proportion of stand composition (MacLean 1980). Mortality in immature stands and spruce stands is much more variable than in mature fir stands, but has been known to reach 70 percent.

White spruce (*Picea glauca* (Moench) Voss), the most widespread spruce variety, is usually considered the second most vulnerable species. Damage to white spruce is generally less severe than to balsam fir, probably because white spruce produces more shoots than fir and these grow significantly larger than fir shoots, thus supplying more food for feeding larvae (Greenbank 1963a).

Red spruce (*P. rubens* Sarg.) and black spruce (*P. mariana* (Mill.) B.S.P.) are the least vulnerable species, in that order. Their relative resistance is due mainly to late opening buds. On the average, red and black spruce buds open 13 days after balsam fir and 9 days after white spruce. In addition, black spruce foliage is not an adequate food source for early instar larvae and many may starve or abandon the tree (Greenbank 1963a).

Budworm also feed on eastern hemlock (*Tsuga canadensis* (L.) Carr.), eastern larch (*Larix laricina* (DuRoi) K. Koch), and eastern white pine (*Pinus strobus* L.). Damage and mortality of eastern hemlock is fairly common in some locations.

Because balsam fir is the species most vulnerable to damage from spruce budworm defoliation, the vulnerability of forest stands increases with increasing amounts of mature and overmature fir (Graham and Orr 1940; Balch 1946; McLintock 1948; Morris and Bishop 1951; Turner 1952; Westveld 1954; Batzer 1969; Van Raalte 1972; Baskerville 1975a; Brown et al. 1976; and Mott 1980). By the same token, vulnerability decreases as the percentage of nonhost species increases. If host trees are overtopped by nonhost trees, vulnerability is further decreased. Such situations often occur in pioneer hardwood stands where a softwood understory is developing. These stand composition variables are the only stand characteristics that have a reasonably consistent relationship with vulnerability to budworm damage over time and among locations.

Although the presence of mature and overmature balsam fir increases vulnerability, it does not follow that immature fir is immune to damage. In general, immature fir stands are less vulnerable, but examples of extensive damage occurring in such stands have been reported (Baskerville 1960; Hatcher 1964; Baskerville and MacLean 1979). In fact, instances of severe budworm damage in young stands seem to be more prevalent during the most recent outbreak, and have been observed in Maine, New Brunswick, Nova Scotia, and Newfoundland, among other areas.

Vulnerability tends to decrease with increasing tree and stand vigor (Craighead 1925; Balch 1946; McLintock 1948; Turner 1952; Westveld 1954; Bean and Batzer 1956) as expressed by growth rate and crown development. These in turn are a function of site quality and growing conditions.

Some studies (Craighead 1925; Balch 1946; Morris and Bishop 1951; Crook et al. 1979; Batzer and Hastings 1981; and others) have shown that as stand density increases, so does vulnerability. Undoubtedly this is also related to tree and stand vigor cited above. Density may also affect the migrating patterns of dispersing larvae, with greater dispersal losses occurring in more open stands (Craighead 1925; Mott 1963; Morris and Mott 1963). In a few relatively recent cases, however, purposely thinned stands of spruce and fir have been severely defoliated and damaged. Perhaps these stands were opened too much, providing optimum conditions for larval development (Mott 1963), as well as for tree growth. It is now apparent that protection (spraying) may be required in young spruce-fir stands that are thinned to optimize growth and subsequently suffer severe budworm defoliation, or else substantial mortality and growth loss will occur.

Vulnerability of individual spruce and fir trees also increases when they are in a subordinate crown position relative to other host trees (Craighead 1925; Blais 1958; Morris and Mott 1963). Witter et al. (1983) listed some additional factors that affect stand vulnerability, many of which are related to those mentioned above (Table 1).

Silvicultural Goals

The relationships between stand characteristics and vulnerability we have described can be used to develop general silvicultural goals. Flexner et al. (1983) listed the following goals for individual stands in the Lake States:

1. Shorten the rotation age of fir to 50 years or less;
2. Reduce the fir content of the stand;
3. Maintain a mixed-species composition whenever feasible;
4. Convert the stand to less susceptible species.

Blum and MacLean (1984) prescribed essentially the same goals with the addition of "maintaining a vigorous stand with rapid growth rates." Achieving these goals should produce a general reduction in vulnerability. As stated previously, however, this reduction in vulnerability

Table 1
Factors that increase the amount of damage (volume loss and tree mortality) occurring in spruce-fir stands during severe spruce budworm outbreaks (from Witter et al. 1984)

General factor[a]	Condition leading to severe damage
Species composition	Stands with large balsam fir components have greater potential for mortality than stands comprised mostly of spruce or hardwoods.
Stand age	Mature fir stands (60 years or older).
Stand density	High basal area of balsam fir, red spruce, and white spruce.
Stand structure	Open stands in which spike tops of host species protrude from the forest canopy.
Stand size	Extensive stands of mature host trees (except black spruce).
Stand location	Stands located downwind (often east) of current outbreak areas.
Topography and latitude	Stands growing at elevations lower than 700 m (2,300 ft) south of 50° latitude.
Site condition	Poorly drained stands, abnormally dry or wet.
Intensity and duration of outbreak	Stand mortality increases with the severity and length of outbreak.

[a] The factors are not listed by order of importance.

cannot be quantified; this should be an important objective of future research.

In the absence of budworm, achieving these goals would enhance the production of high-value wood products and the maintenance of a vigorous forest cover. A question posed by Blum and MacLean (1984) is this: If we know that there is a high probability of a budworm outbreak occurring during a rotation, and that damage to the forest stand is likely to occur regardless of achieving the above goals, what additional benefits might accrue from reducing vulnerability?

If a sizable portion of the forest is in a less vulnerable condition, resulting in less mortality and growth loss, the need for direct control (spraying) should be reduced and the time interval between spray operations can be lengthened (Mott 1980; Dimond et al. 1984). A less vulnerable forest should also allow more time for shifting salvage operations to the most vulnerable stands as mortality commences. Also, the glut of salvaged material that occurs at the height of the infestation should be somewhat reduced (Blum and MacLean 1984). Perhaps most important, the forest stands should be in a vigorous, healthy condition that will enable them to respond favorably to direct control programs once an infestation is underway (Dimond et al. 1984)

Silvicultural Treatments to Meet Goals

To begin with, areas within the range of the budworm differ considerably, not only in the makeup of the forest resource (Mott 1980) and ownership, but also in their marketing, economic, and social environment (Irland and Runyon 1984). Consequently, the opportunity to implement an intensive silvicultural program varies from place to place. In addition, not all areas in a given ownership will warrant such an effort. Site productivity, accessibility, and present stand condition are probably the most common limiting factors throughout the budworm's range (Blum and MacLean 1984).

The availability of recent inventory data, type maps, and site productivity information is also quite variable. These information sources are invaluable aides for identifying candidate stands for silvicultural treatments. The most logical place to direct silvicultural investment in altering the species composition of existing stands is on high-quality, accessible sites. Fully mature or overmature stands having a good proportion of spruce or nonhost species probably require the least investment because marketable products can be removed, whereas sapling and pole stands offer the best opportunity because they have more stems to choose from, generally greater vigor, and somewhat less windthrow potential (Blum and MacLean 1984; Irland and Runyon 1984).

The relative tolerance of spruce and fir trees permit the use of either even-aged or uneven-aged silviculture (Frank and Bjorkbom 1973; Flexner et al. 1983). A general description of the various systems follows; a number of handbooks and silvicultural guides are available for detailed prescriptions to be followed in specific regions (e.g. Blum et al. 1983; Flexner et al. 1983; Montgomery et al. 1982a, b; Frank and Blum 1978; Frank and Bjorkbom 1973).

Uneven-aged Silvicultural Systems

The selection system of silviculture and the maintenance of an uneven-aged stand structure were widely promoted for reducing vulnerability to budworm in the 1940s and early 1950s (Balch 1946; Westveld 1946, 1954; McLintock 1947). Many spruce-fir stands acquire the appearance of an uneven-aged structure due to the differential vulnerabilities of spruce and fir to budworm damage, the tolerance of both species to shade, the shorter life span of fir even in the absence of budworm, and those early cutting practices when both "loggers choice" and diameter limit cutting differentiated between species on the basis of size. This was especially true in the southern portion of the spruce-fir range and in Maine where red spruce is an abundant species (Mott 1980).

Reduction of the balsam fir component was the basic theme behind the use of the selection system to lower the vulnerability of forest stands. A key to the success of the system is repeated, relatively light harvests that create openings for regeneration. Experience indicates that the selection system of silviculture can be an effective tool in altering species composition (Frank and Bjorkbom 1973; Blum 1978; Frank and Blum 1978). However, this form of silviculture maintains a continuous, deep-crowned, mature or nearly mature canopy with abundant sun foliage and flowering (Baskerville 1975b). Trees making up this canopy are highly vulnerable to budworm damage in a relative sense, even if predominantly red spruce. Once infested, the overstory serves as a reservoir of larvae that disperse downward, exposing younger age classes to damage. To quote Baskerville (1975b) "The net result of the practice of selection forestry would be the preservation of large areas of mature forest which would be ideal for budworm survival. It would appear that the concept of the selection forest has no place in management for control of the budworm."

The selection system is somewhat more complicated than even-aged systems because a given stand structure goal must be adhered to and the desired mixture of age and size classes maintained. Harvesting must cover larger areas to meet a given allowable cut and harvested trees should be marked in advance. The need for detailed stand-by-stand record keeping is greater.

Nevertheless, both individual tree and group selection are still recommended in some situations (Schmitt 1982; Flexner et al. 1983; Blum 1984; Blum and MacLean 1984). Selection may be the only system allowable in some areas, such as streamside buffer strips, along roadsides where esthetics are important, or in deer wintering areas. Also it is probably the only system that can be used on small ownerships to yield a reasonably consistent return. In these situations, special protection approaches will probably be needed to meet management goals during severe infestations (Blum 1985; Blum and MacLean 1984).

Even-aged Silvicultural Systems

Even-aged silvicultural systems are the most commonly used in eastern spruce-fir today. Applicable regeneration methods include clearcut harvesting in blocks and patches, clearcut harvesting in strips, and shelterwood harvesting (Frank 1979; Montgomery et al. 1982a, b; Schmitt 1982; Flexner et al. 1983; Blum 1984) (Table 2).

During an active budworm infestation, stands to be regenerated may require intensive suppression efforts to promote seed production regardless of the regeneration method used (Ghent 1958).

Clearcut Harvesting

Clearcut harvesting in blocks, patches or narrow strips is recommended for mature, overmature, or insect and disease-ridden stands where vulnerability to budworm damage is high and where partial harvesting could result in mortality or damage to residual trees (Westveld 1953; Frank and Bjorkbom 1973). Mature stands that are predominantly fir are good candidates for some form of clearcut harvesting, as are those on sites where wind damage to the residual stand would be potentially high. Clearcut harvesting is an efficient system of harvesting, especially with highly mechanized equipment.

Natural regeneration can often be relied on to restock a clearcut area. However, success is critically dependent upon the presence of advance regeneration. Biologically, a clearcut harvest with advance regeneration present is similar to a shelterwood, but there is no attempt to manipulate the size or species composition of seedlings by means of preparatory harvests as there usually is with the shelterwood system of silviculture (Blum et al. 1983). Seed dispersal from adjacent stands may suffice in smaller clearcut blocks, patches or strips where adequate advance regeneration is absent, but in many cases regenerating these stands will require site preparation and planting (Frank and Bjorkbom 1973; Blum et al 1983; Flexner et al. 1983). Residual overstory trees of spruce budworm host species must be removed from clearcut areas to prevent budworm larvae from dispersing downward to the new regeneration (Blum and MacLean 1984).

In the Lake States, clearcutting followed by natural regeneration is commonly used to convert spruce-fir stands to aspen stands. This method works if the stand contains at least 20 sq. ft. of aspen basal area per acre ($4.6 m^2/ha$). If this is not present, nearby aspen clones may provide for natural seeding (Flexner et al. 1983). Aspen stands established in this manner often develop a fir understory that will comprise the main stand when the aspen is harvested. The aspen overstory will provide some protection to the fir during a budworm outbreak.

In many areas, clearcut harvesting encourages undesirable vegetation such as hardwoods and raspberries

Table 2
Recommended harvesting methods for natural regeneration of spruce and fir (from Schmitt 1982)

Species composition	Advance regeneration	Stand vigor and site	Regeneration method
50% + fir	Ample	Poor, dense stocking	Clearcut
50% + fir	Moderate	Good, windfirm	Stripcut[1]
40% + spruce	Poor or poor in spruce	Good, windfirm	Shelterwood[1]
50% + spruce	Ample, distributed over range of site classes	Moderate, windfirm, appropriate structure	Selection

[1] Budworm protection essential

(*Rubus* spp.) that may inhibit the growth and development of softwood regeneration. Herbicide treatment of these areas may be required, and if regeneration is lacking, planting may be necessary (Westveld 1953; Frank and Bjorkbom 1973). The white spruce type in the Lake States is dependent on planting (Blum et al. 1983).

If excessive seedling losses due to mechanical damage or drastic exposure are anticipated, or advance regeneration is meager, clearcut harvesting may be done in narrow strips or small patches rather than large blocks. Strips may be progressive or alternate and should be no wider than half the height of border trees if shelter is needed, and patches should be about 1 acre (0.4 ha) or less in size. (These are often termed strip and patch shelterwood.) If shelter from drastic exposure is not required, strip width can be as wide as 400 feet (120 m) depending on environmental conditions and the seed dispersal characteristics of border trees (Frank and Bjorkbom 1973). The shelter and seed source provided distinguish this method from ordinary clearcutting, but border trees are a potential source of spruce budworm larvae that may disperse to the regeneration.

Harvesting in strips or patches also increases the species diversity of plants and animals and may encourage natural enemies of the spruce budworm. An example of the latter would be habitat enhancement for trap nesting wasps that prey on budworm larvae (Jennings and Houseweart 1984). Strip clearcutting also enhances dispersal losses of early instar larvae (Jennings et al. 1983).

Shelterwood

The shelterwood system of silviculture is suitable for spruce-fir stands that lack adequate advance regeneration. It is applicable for stands on good sites where vigorous growth can be expected, windthrow potential is minimal, and there are no insect and disease problems of major concern (Frank and Bjorkbom 1973; Blum et al. 1983; Flexner et al. 1983). Overstory trees in this system are gradually removed in two or three stages. Before final removal, these overstory trees supply needed protection until developing seedlings can be safely exposed to full sunlight. Gradually opening the overstory in this manner may also improve windfirmness, and the partial shade provided will inhibit the development of herbaceous growth such as raspberries.

The shelterwood system allows a degree of control over the species composition of the developing regeneration, as long as desired species are well distributed and represented in sufficient numbers in the overstory. An additional benefit of the system is the improved growing conditions provided for the residual overstory, which should be of high quality, vigorous trees. If high populations of spruce budworm are present in the overstory, however, direct suppression of the insect will be required to ensure seed production and to protect developing regeneration from larvae dispersing downward from the overstory.

Stand Conversion

Stand conversion and the creation of monocultures have many economic and biological ramifications which vary considerably across the range of the spruce budworm. Certainly, stand conversion is desirable if nonhost or less vulnerable species will fill the landowner's needs. Throughout most of the spruce-fir region there have been numerous recent advances in site preparation, planting techniques, improved planting stock, and techniques for controlling competing vegetation that are beyond the scope of this paper. Although relatively expensive (Irland and Runyon 1984), planting to nonhost or less vulnerable host species on the best sites will decrease vulnerability and susceptibility to spruce budworm and improve long-term yield. Of the host species, black spruce is the most promising. An estimated 17,300 acres (7 000 hectares) were planted in Maine in 1983 (USDA For. Serv. 1983). Areas planted in eastern Canada in 1980 included 30 000 ha (76,107 acres) in Ontario, 14 100 ha (34,841 acres) in Quebec, 15 700 ha (38,795 acres) in New Brunswick, 2 700 ha (6,672 acres) in Nova Scotia, and 180 ha (445 acres) in Newfoundland (Brace and Golec 1982). These areas have increased since 1980, and are expected to increase further in future years. However, it is unreasonable to assume that wholesale conversion of large regions will be either feasible or desirable.

Prescribed burning has been used for site preparation and hazard reduction for both planting and natural regeneration. Total acreages burned have been relatively small, and in the eastern United States the technique is largely experimental.

Thinnings or Intermediate Harvests

It cannot be overemphasized that a silvicultural effort to reduce the vulnerability of spruce-fir stands to budworm damage is a long-term proposition. Just as in any intensive silvicultural program, this entails a regime of intermediate harvests or thinnings over the rotation (Westveld 1953; Frank and Bjorkbom 1973; Batzer 1976). If regeneration is adequate and well distributed, these operations will allow manipulation of species composition to the detriment of fir in fir-hardwood and fir-spruce stands. On the best sites, a 10-year operating interval is probably the shortest that is practical, although the time period will vary up to 20 years depending on stand growth achieved, accessibility, and operational constraints (Frank and Bjorkbom 1973; Batzer 1976; Blum and MacLean 1984).

Precommercial thinnings or cleanings, when the stands are in the sapling or small pole stage, can cause a dramatic change in species composition in the residual stand provided desirable, less vulnerable species are present in sufficient numbers and well-distributed. Precommercial thinning also improves spacing around residual trees and accelerates individual tree growth (Frank and Bjorkbom 1973; Frank 1979; Piene 1981).

The primary goals of intermediate harvests, besides removing fir to the extent feasible, should be to 1) provide adequate growing space for individual trees, 2) remove trees that may not survive to the next harvest, and 3) avoid creating large holes or openings in the canopy that may decrease windfirmness (McLintock 1954; Frank and Bjorkbom 1973; Falk 1980; Flexner et al. 1983; Blum and MacLean 1984). In most cases, first priority should be thinning from below (removing trees in a subordinate crown position) followed by spacing in the main crown canopy. Even pure balsam fir stands can be reduced in vulnerability if they are kept vigorous by thinning (Turner 1952; Westveld 1954; Bean and Batzer 1956).

Some of the disadvantages of partial harvesting are (Irland and Runyon 1984):

1. Risk of increased wind damage in residual stand.
2. Lower volume per acre cut; somewhat higher logging cost.
3. Greater expense in sale preparation and logging supervision.
4. May require more new roads than clearcutting.
5. There is no guarantee that residual spruce stands will survive further feeding (i.e., protection of the residual stand may be required).

Wind damage following partial harvesting is the cause of considerable apprehension among foresters and land managers in the spruce-fir region. The potential for wind damage varies considerably depending on site and soil characteristics, the amount of overstory removed in the harvest, and the past management of the stand (McLintock 1954). To enhance windfirmness, harvests should be relatively light (perhaps no more than one-third of the basal area removed); however, this is a matter of judgement. If past management has kept the stand vigorous, well spaced and fast growing, windfirmness should follow naturally. McLintock (1954), Falk (1980), Schmitt (1982), and Flexner et al. (1983) thoroughly discuss the apparent causes of wind damage and make specific recommendations for minimizing it. Flexner et al. (1983) summarized these recommendations as follows:

1. Regardless of how sound they appear, fir larger than 8 in. (20 cm) dbh are often rotten and should not be left after a partial harvesting operation.
2. Stands growing on the flanks and lower slopes on the lee side of hills are especially vulnerable to turbulent winds.
3. Stands taller than 40 ft (12 m) are more apt to suffer wind damage than shorter stands.
4. Wind striking stand edges can be deflected up to 90 degrees and accelerated up to 25 percent. Cutting boundaries that create corners or obvious indentations should be avoided because they funnel winds and concentrate their force.
5. Edges of open stands, where wind can penetrate easily, provide better protection than edges of a dense stand.
6. In mixed hardwood-conifer stands, wind damage following partial cutting is reduced if the hardwood component is well distributed and left uncut.
7. Wind damage is often more severe in stands on shallow soils, where the water table, bedrock, or fragipan are within several feet of the surface.

The possibility exists that budworm damage per se can increase the risk of wind damage. Redmond (1959) found that heavy defoliation of balsam fir resulted in rootlet mortality of over 75 percent. What role rootlets play in anchoring trees in the soil is uncertain, but there is ample evidence that root rot increases the incidence of wind damage (Falk 1980).

Salvage and Presalvage Operations

Flexner et al. (1983) define a salvage operation as "the removal of trees that have been killed or damaged by injurious agents other than competition from other trees," and a presalvage operation as "a form of salvage which reduces economic losses by removing highly vulnerable trees in anticipation of damage."

The long-term silvicultural tactics previously discussed are designed to reduce the overall vulnerability of spruce-fir stands to budworm damage, and to that extent could be considered a form of presalvage by the above definition. However, even the most intense, long-term silvicultural program will not eliminate the need to accelerate presalvage and salvage efforts in the face of a budworm outbreak, unless anticipated losses are allowed for in a sustained yield program. The primary objective of salvage operations is to harvest dead and dying trees while they can still be used, thereby reducing the economic consequences of the infestation. Integrated with chemical, biological, and long-term silvicultural protection measures, salvage should also reduce the impact of a severe outbreak on forest management goals such as sustained yield regulation (Blum and MacLean 1984). There are those, however, who would argue that in many cases, salvage can be counterproductive (Dimond et al. 1984) and that dead trees should never be cut, since it is only by cutting live trees that any impact may be had on budworm habitat and on future treatment costs (Irland and Runyon 1984).

Nonetheless, it is very important that both protection and salvage activities be considered as integrated parts of long-term management, especially in terms of maintaining a regulated age class distribution. Otherwise, the need to salvage areas of dead and dying forests can result in loss of control over the sustained-yield age class distribution (Blum and MacLean 1984). As discussed by Dimond et al. (1984), if enough area cannot be economically protected to meet wood supply needs, the harvest must be reduced to a level that can be sustained. The only alternative is to acknowledge that a sustained yield is not possible, in which case salvage operations on unprotected land will delay the inevitable for a few years.

The decision to salvage or not will also be influenced by 1) the cost of harvesting the wood (dead wood is particularly expensive to harvest if it has deteriorated somewhat (see Sewell and Maranda 1978), 2) the present and future need and capacity for using the wood, 3) the protection options available, and 4) the risk of damage if the wood is allowed to stand unprotected (Blum and MacLean 1984; Dimond et al. 1984; Irland and Runyon 1984).

As previously stated, the objective of a salvage operation during a budworm outbreak is to harvest dead and dying trees before they deteriorate and can no longer be used. The length of time balsam fir can be used depends on the intensity of attack by secondary insects, the rate of sap stain and sap rot development, and local climatic conditions (Basham 1984). A reasonable estimate of the length of usefulness is 1 to 3 years after death, although this depends on locality, and may be up to 5 years in some areas (Flexner et al. 1983; Basham 1984).

Salvage Priorities

The first step in planning and implementing a salvage operation on an ownership is to determine which stands need to be salvaged. Hazard ratings and insect monitoring systems are useful for this purpose (MacLean 1980, 1982; Montgomery et al. 1982a). The details of hazard rating systems vary somewhat depending on how and where they were developed, but the accuracy of almost all of them depends on having an adequate forest inventory (Blum and MacLean 1984). The finer the species breakdown, especially among host tree species, the better. Estimates of maturity or stand age should also be made. Site productivity, stand volume or basal area, stand isolation, tree condition, and past infestation pattern may all be useful information in rating damage potential, particularly in the absence of formal hazard rating or insect monitoring systems (Flexner et al. 1983; Blum and MacLean 1984).

Once stands have been ranked according to their damage potential, other factors come into play. These include accessibility, treatment alternatives, harvesting resources available, available markets, and social or political constraints. It should be possible to salvage in an orderly fashion while implementing some basic silvicultural principles, although in haste. Early detection of an impending infestation will allow some lead time for planning and implementing salvage procedures (Flexner et al. 1983; Blum and MacLean 1984). Both Dimond et al. (1984) and Flexner et al. (1983) discuss harvesting priorities in some detail, in terms of stand characteristics and forest management criteria.

Dimond et al. (1984) presented a priority system to guide harvest planning decisions. This system is based primarily on future growth potential and response of individual trees to spray treatments, rather than on their vulnerability to budworm damage if left unprotected. In this sense the system is not strictly one of salvage priorities, but is an essential element in an integrated pest-forest management program.

Silvicultural Options

Silvicultural options in a salvage situation are dictated by present condition of the individual stands involved, assuming minimal harvesting constraints. It makes no sense, for instance, to salvage all mature fir in a partial harvest or to make a first stage shelterwood harvest if it is obvious that the amount of vulnerable material removed will result in excessive wind damage. The better alternative would probably be to clearcut and regenerate, or leave enough volume to reduce wind damage risk and chemically protect the vulnerable residual stand.

One possible array of short-term silvicultural options is presented in Table 3. In addition, Mott (1980) proposed a strategy for the state of Maine based on a fir-only harvest coupled with targeted spraying. This strategy, although perhaps not strictly salvage or presalvage, contained elements of both, and is basically a transitional strategy leading to a less vulnerable forest condition.

Whatever mix of options is used, however, depends greatly on individual circumstances. The ability to harvest and utilize the wood economically, and the technology to protect stands precisely are important. Although it is impossible to eliminate economic considerations from forest operations, silvicultural options should be judged in light of their long-term effects as well as their immediate economic benefits.

Table 3
Array of short-term silvicultural options available in a salvage situation (Blum and MacLean 1984)

Stand vulnerability rating	Site quality	Silviculture options	Probable need for protection in short term
High	Good	Regenerate:	
		1) Block clearcut, natural regeneration	Low
		2) Clearcut, plant	Nil
		3) Shelterwood	High
		Partial harvest, spruce and fir priority	High
		Do nothing (abandon to budworm)	High
	Poor	Regenerate:	
		1) Block clearcut, natural regeneration	Low
		Partial harvest	High
		Do nothing	Low
Medium	Good	Regenerate:	
		1) Block clearcut, natural regeneration	Low
		2) Strip clearcut, natural regeneration	Medium-low
		3) Clearcut, plant	Nil
		4) Shelterwood	Medium
		Partial harvest, spruce and fir priority	Medium-low
		Do nothing	Medium-low
	Poor	Regenerate:	
		1) Block clearcut, natural regeneration	Low
		2) Strip clearcut, natural	Medium-low
		3) Shelterwood	Medium-low
		Partial harvest, spruce and fir priority	Medium-low
		Do nothing	Low

Table 3 **(concluded)**

Low	Good	Regenerate:	
		1) Block clearcut, natural regeneration	Low-nil
		2) Strip clearcut, natural regeneration	Low-nil
		3) Clearcut, plant	Nil
		4) Shelterwood	Low-nil
		Partial harvest	Low-nil
		Do nothing	Low-nil
	Poor	Regenerate:	
		1) Block clearcut, natural regeneration	Nil
		2) Strip clearcut, natural regeneration	Nil
		3) Shelterwood	Nil
		Partial harvest	Nil
		Do nothing	Nil

Long-Term Regional Management Strategies

Long-term regional management strategies include the silvicultural tactics already discussed, but the major concern is outbreak development over an entire region rather than damage to a particular stand. Two generalities have historically stood out in the literature as major components of outbreak development: 1) extensive contiguous tracts of mature or overmature balsam fir, and 2) periods of relatively dry weather during the larval stage when mature trees are flowering heavily (Balch 1946; Prebble and Morris 1951; Turner 1952; Morris 1958; Mott 1963; Blais 1973; Baskerville 1975b, 1976; Flexner et al. 1983, and others). Recent detailed study of the population dynamics of spruce budworm by Royama (1984) has questioned these generalities, and indicated that budworm populations in different areas appear to oscillate in synchrony, regardless of level of damage to the forest, because of correlation of climatic variables among sites. The cause of oscillation of budworm populations appears to be linked to an array of incompletely understood diseases and parasites affecting the population (Royama 1984), and research is currently ongoing to test this theory. Regardless of the cause of budworm outbreaks, it is clear that the most severe damage occurs in large contiguous areas of mature balsam fir, and regional management strategies largely involve reducing the area of this forest type.

At the regional level, area effects come into play. The spatial distribution of individual stand types, and the distribution of age classes of stands become the most important characteristics that can be controlled. Regional planning involves many stands, which cover large areas in different ownerships and political jurisdictions; the scale of treatments, complications, and regulatory requirements for actual implementation are increased many times. Effective management strategies must supercede political or ownership boundaries, and coordination is essential. Epidemiology or outbreak dynamics of the spruce budworm also become important. Dispersal patterns for instance, may be influenced by prevailing wind and weather patterns, or geographic features, as well as the character of the forest resource (Blum and MacLean 1984).

Encouraging between-stand diversity, in terms of both age-class distribution and species composition, is the key element in management policy for regions or large properties. A variety of young and old, vulnerable and nonvulnerable, host and nonhost stands distributed over a region would lessen the impact of an outbreak on the wood supply (since fewer stands would be in a vulnerable condition) and would also decrease losses from individual stands. The goal of diversifying is to create a patchwork of young stands, recent clearcuts, nonhost and nonvulnerable stands interspersed with more vulnerable stands. Accomplishing this is not simple. It requires a long-term, sustained regulatory effort that is coordinated amongst the various jurisdictions, particularly the timing and location of harvesting. It is further complicated by operational and accessibility factors.

Recent and ongoing research into the population dynamics and epidemiology of the spruce budworm (Blais 1983a; Hardy et al. 1983; Royama 1984) has altered some of the traditional theories regarding oscillations in budworm populations. Some of the conventional wisdom regarding the prerequisites for a severe infestation (i.e., extensive areas of mature fir) may well be suspect. Changes in theories of budworm population dynamics will affect both forest protection (spraying) strategy and silvicultural and management strategies. Suffice it to say, however, that more research is needed to develop and test these theories.

Regional Manipulation of Age-Class Structure

Regional management, to reduce vulnerability, should give a high priority to the attainment of a balanced, regulated age-class distribution. This may even require abandoning specific areas of the forest to the budworm, allowing them to be recycled to younger age classes, if present levels of harvesting are insufficient to attain regulation. Stands thus recycled to younger age classes, whether by harvesting, budworm or other means, should be spatially arranged to achieve the patchwork of age classes, species mix, and vulnerability levels previously mentioned.

Attaining a regulated, sustained yield forest with a balanced age class distribution is probably the strategy with the best potential for reducing vulnerability (and perhaps susceptibility) on a regional basis. Young stands in general suffer less damage from a given level of attack, and offer less favorable egg-laying sites for budworm moths, which prefer to lay their eggs on the tallest, most exposed trees (Greenbank 1963b). On an areal basis, less damage will occur with a mixture of vulnerable and nonvulnerable stands. The spatial distribution will also promote dispersal losses of the small larval stages of the insect (Mott 1963).

Regional Manipulation of Species Composition

Significantly changing the species composition on a regional basis is a much more difficult task than altering age-class distribution because of the large areas involved. Significantly changing composition in the short-term is a practical impossibility, even with an intensive program of site preparation and planting coupled with harvesting practices that select against vulnerable species. A regional approach entails millions of acres, many of which will be left untreated in a given year and often regenerate to vulnerable spruce-fir. Clearcutting, fire protection, and repeated budworm attacks have probably all worked toward increasing the amount of balsam fir, the most vulnerable species (Baskerville 1975a; Blais 1983a; MacLean 1984).

Manipulating species composition on a regional basis requires intensive efforts on large areas over a long-period of time. A two-fold attack is suggested:

1. If consistent with management goals, include nonhost species in planting programs and ensure that both harvesting and planting are used to enhance between-stand diversity. It would be wise to observe the usual cautions against the creation of large areas of single-species plantations because virtually any tree species can develop some kind of insect or disease problem.
2. Discriminate against balsam fir whenever possible on both a whole-stand and individual tree basis. Preferential harvesting of fir stands rather than spruce or nonhost stands, cutting fir to a smaller diameter limit, and planting to nonhost species are all possibilities.

It should be remembered that management strategies will vary from one region to another. There are differences in both budworm outbreak dynamics (Hardy et al. 1983) and damage patterns (Blais 1968, 1983a; MacLean 1985) between regions. Markets, utilization, and forest types vary among diverse regions from the Lake States to Newfoundland. These factors will modify regional management strategies.

Protection of specific areas of the region with insecticides is essential to maintain wood supply. Even in the absence of large-scale spray programs, high value silviculturally treated stands, plantations, seed production areas, and genetic breeding stock must be protected. Protection is also necessary to maintain the age-class distribution already discussed (Blum and MacLean 1984).

Implementation Experience

Various of the silvicultural tactics and regional management strategies discussed in this paper are being used in most of the eastern Canadian provinces and U.S. states currently suffering budworm damage. However, the areal extent of usage is generally very small, and the variation among ownerships within a given region, let alone between regions, is extremely high. Thus it is difficult to generalize about implementation experience. It is also difficult to obtain recent data about the extent of silvicultural activity in many regions.

Reed and Associates (1978) carried out a comprehensive review of forest management in Canada, and described the current state of management in each province. They concluded that at best, management is minimal and large areas receive little or no management. This was felt to be the result of a lack of commitment to forest management as a requirement for staying in business, as well as a lack of funds for the necessary programs. Similarly, Weetman (1982) reviewed corporate silvicultural activity in Canada, and concluded that most companies practiced "extensive" or "basic" level silviculture, with only a few pioneering companies applying "intensive" silviculture, which was defined to include activities such as stand tending, integrated pest management, and 20-year planning. Using a case study approach, Reed and Associates (1978) demonstrated that above average standards of management were achieved in those areas where industry has reasonable security of tenure, good cooperation with the provincial governments, and could offset some of the management costs against stumpage or obtain an immediate benefit from management. These points clearly demonstrate the influence of economic factors on management plans designed to cope with spruce budworm damage.

Areas of productive forest land, annual harvesting, and annual silviculture and protection activities are summarized for each of the eastern Canadian provinces in Table 4. These data indicate that the amount of site preparation, planting, and stand tending (thinning, chemical and mechanical cleaning, etc.) represents only a relatively small proportion of the annual harvest area in most provinces. Spruce budworm control operations were primarily in New Brunswick and Quebec (Table 4). The data in Table 4 represent an average for the 1975-80 period, which were the most recent available, but activities in some provinces may have increased substantially since that time.

The 1983 Spruce Budworm Environmental Assessment for Maine listed the major objectives of Maine landowners and managers, gleaned from a number of individual integrated pest management plans (USDA Forest Service 1983). As expected, the silvicultural actions anticipated under these plans were stand-oriented rather than regional in nature, although some objectives listed were apropos to both. Objectives included:

1. Reducing the amount of fir and increasing the percentage of spruce in softwood stands, through both precommercial and commercial operations.
2. Breaking up the age-class distribution, by managing fir on a short rotation, and reducing the forest area made up of the large age-class resulting from the 1910-1919 budworm outbreak.
3. Salvaging dead and dying trees, to recover fiber before decay renders it useless, and to reduce fire hazard and secondary insect problems.
4. Keeping some stands alive by application of insecticide, including those in jeopardy of being killed in the next 2 to 5 years plus stands whose retention is necessary to balance the age classes in the next rotation.
5. Obtaining better information on the composition and condition of the forest resource, by intensifying mapping and inventory work.

Table 4
Summary of annual silviculture statistics for each eastern Canadian province, averaged for the 1975-80 period (modified from Brace and Golec 1982)

Province	Area of productive forest land[1]		Area harvested		Area of site preparation		Area planted		Area of stand tending[2]		Area of pest control[3]	
	('000 ha)	('000 acres)	(ha)	(acres)	(ha)	(acres)	(ha)	(acres)	(ha)	(acres)	(ha)	(acres)
Ontario	42 600	105,265	191 010	471,986	46 889	115,863	28 221	69,734	42 390	104,746	18 507	45,731
Quebec	84 900	209,788	195 616	483,367	7 488	18,503	15 184	37,520	NA	NA	1 780 000	4,398,380
New Brunswick	6 200	15,320	(92 580)[4]	(228,765)[4]	13 900	34,347	10 146	25,071	3 322 [5]	8,209 [5]	2 282 000	5,638,822
Nova Scotia	2 900	7,166	29 541	72,996	1 388	3,430	2 190	5,411	2 432	6,009	11 396	28,159
Prince Edward Island	300	741	1 636	4,043	126	304	108	267	4	10	0	0
Newfoundland	8 500	21,003	(16 000)	(39,536)	371	917	37	91	1 589	3,926	91 876	227,026

[1] From Bonnor (1982)

[2] All methods of stand tending, including thinning, chemical and mechanical cleaning, etc.

[3] Mainly spruce budworm control

[4] Numbers in parentheses are estimates

[5] 1979-80 data only

In addition, landowners in Maine were polled prior to 1983 for an estimate of acreage that would fall into the various integrated pest management components. These are shown in Table 5.

The Future

Quantifying the results of silvicultural actions is a continuing problem, particularly in terms of the reduction in vulnerability achieved. In many cases, the treatments are poorly defined concerning type, timing, location, and amount. We know that many actions such as removing fir, increasing less vulnerable or nonhost species, and maintaining larger amounts of less vulnerable age classes help reduce vulnerability. Whether the reduction can be quantified or not, the logic of implementing these procedures cannot be denied.

On the other hand, quantification of the effects of silvicultural treatments on vulnerability is essential for choosing among various treatment mixes, determining the cost effectiveness of treatments, predicting future yields for management planning, and estimating levels of protection needed for the future forest.

The development and testing of new theories regarding population and outbreak dynamics holds exciting possibilities for future treatment strategies, both within stand and regional. This research must be brought to fruition for the potential to be realized.

There are encouraging developments on almost every front — growth and yield prediction, hazard rating systems, harvesting techniques, markets and utilization, and budworm biology that will all influence silvicultural recommendations in the future. These developments should work in concert to bring us closer to rendering budworm outbreaks much less potent in the future.

Literature Cited

Balch, R.E. 1946. The spruce budworm and forest management in the Maritime Provinces. Can. Dept. Agric., Div. Entomol., Ottawa. Publ. No. 60. 7 p.

Basham, J.T. 1984. Degradation and loss of wood fibre in spruce budworm-killed timber, and effects on utilization. For. Chron. 60:10-14.

Baskerville, G.L. 1960. Mortality in immature balsam fir following severe budworm defoliation. For. Chron. 36:342-345.

Baskerville, G.L. 1975a. Spruce budworm: super silviculturist. For. Chron. 51:138-140.

Baskerville, G.L. 1975b. Spruce budworm: the answer is forest management: or is it? For. Chron. 51:157-160.

Baskerville, G.L., ed. 1976. Report of the task force for evaluation of budworm control alternatives. New Brunswick Dep. Nat. Resour., Fredericton, N.B. 210 p.

Table 5
Estimated acreages of various components of IPM for 1983 among Maine landowners/land managers involved in spruce budworm suppression activities (Modified from USDA Forest Service 1983)

Component	Acres	Hectares	Ancitipated trend over 5-year period[1]
Harvesting:			
Partial cutting	75,335	30 511	=
Clearcutting	87,138	35 291	+
Cable yarding system	100	41	+
Thinning and release commercial and precommercial:			
Chain saw and brush saw	5,050	2 045	+
Herbicide application	23,700	9 589	+
Planting:			
Site preparations	4,450	1 802	+
Planting	17,300	7 007	+
Insecticide application:			
Chemical insecticides	765,000	309 825	–
B.t.	135,000	54 675	+

[1] = will remain about the same
+ will increase
– will decrease

Baskerville, G.L. 1982. The spruce/fir wood supply in New Brunswick. For. Manage. Br., New Brunswick Dep. Nat. Resour., Fredericton, N.B. Rep. No. 0-88838-408-4.

Baskerville, G.L.; MacLean, D.A. 1979. Budworm-caused mortality and 20-year recovery in immature balsam fir stands. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B.: Inf. Rep. M-X-102. 23 p.

Baskerville, G.L.; Montgomery, B.A. 1983. Spruce budworm information leaflets for the Lake States V. Forest management. Mich. Coop. For. Pest Manage. Progr., East Lansing, MI: Leaflet 83-11. 2 p.

Batzer, H.O. 1969. Forest character and vulnerability of balsam fir to spruce budworm in Minnesota. For. Sci. 15:17-25.

Batzer, H.O. 1976. Silvicultural control techniques for the spruce budworm. Pages 110-116 *in* H.W. Klein, tech. coord. Proc. Symp. Spruce Budworm. U.S. Dep. Agric., For. Serv., Washington, DC. Misc. Pub. 1327.

Batzer, H.O.; Hastings, A.R. 1981. Rating spruce-fir stands for spruce budworm vulnerability in Minnesota. Pages 105-108 *in* R.L. Hedden; S.J. Barras; J.E. Coster; tech. coords. Hazard-rating systems in forest insect pest management: symposium proceedings. U.S. Dep. Agric., For. Serv., Washington, DC.: Gen. Tech. Rep. WO-27.

Bean, J.L.; Batzer, H.O. 1956. A spruce budworm risk rating for the spruce fir types in the Lake States. U.S. Dep. Agric., For. Serv., Lake States For. Exp. Stn., St. Paul, Minn. Tech. Note LS-453, 2 p.

Blais, J.R. 1954. The recurrence of spruce budworm infestations in the past century in the Lac Seul area of northwestern Ontario. Ecology 35:62-71.

Blais, J.R. 1958. The vulnerability of balsam fir to spruce budworm attack in northern Ontario, with special reference to the physiological age of the tree. For. Chron. 34:405-422.

Blais, J.R. 1968. Regional variation in susceptibility of eastern North American forest to budworm attack based on history of outbreaks. For. Chron. 44:17-23.

Blais, J.R. 1973. Control of spruce budworm: current and future strategies. Bull. Entomol. Soc. America. 19:208-213.

Blais, J.R. 1983a. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13:539-547.

Blais, J.R. 1983b. Predicting tree mortality induced by spruce budworm: a discussion. For. Chron. 59:294-297.

Blum, B.M. 1978. Regeneration and uneven-aged silviculture — the state of the art. Pages 67-88 *in* Uneven-aged silviculture and management in the United States. Part II. U.S. Dep. Agric., For. Serv., Timber Manage. Res., Washington, DC.

Blum, B.M. 1985. Appropriate silviculture. *In* Proc. Symp. Spruce-fir management and spruce budworm. 2nd SAF Region VI Tech. Conf. 24-26 April 1984, Burlington, VT. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-99. 217 p.

Blum, B.M.; Benzie, J.W.; Merski, E. 1983. Eastern spruce-fir. Pages 128-130 *in* Burns, R.M., tech. comp. Silvicultural systems for the major forest types of the United States. U.S. Dep. Agric., For. Serv., Washington, DC: Agric. Handb. 445, Revised.

Blum, B.M.; MacLean, D.A. 1984. Silviculture, forest management and the spruce budworm. Chapter 6 *in* D.M. Schmitt; D.G. Grimble; J.L. Searcy; tech. coords. Managing the Spruce Budworm in Eastern North America. U.S. Dep. Agric., For. Serv., Washington, DC: Agric. Handb. 620.

Bonner, G.M. 1982. Canada's forest inventory 1981. Can. For. Serv., For. Stat. Syst. Br., Chalk River, Ont. 79 p.

Brace, L.G. and P.J. Golec. 1982. Silviculture statistics for Canada, 1975-80. Can. For. Serv., North. For. Res. Cent., Edmonton, Alta. Inf. Rep. NOR-X-245. 48 p.

Brown, M.W.; Knight, F.B.; Dimond, J.B. 1976. Stand composition and susceptibility to spruce budworms epidemics. Univ. Maine, Sci. For. Res. Tech. Note 61. 4 p.

Craighead, F.C. 1925. Relation between mortality of trees attacked by the spruce budworm (*Cacoecia fumiferana* Clem.) and previous growth. J. Agric. Res. 30:541-555.

Crook, G.W.; Vezina, P.E.; Hardy, Y. 1979. Susceptibility of balsam fir to spruce budworm defoliation as affected by thinning. Can. J. For. Res. 9:428-435.

Dimond, J.B.; Seymour, R.S.; Mott, D.G. 1984. Planning insecticide application and timber harvesting in a spruce budworm epidemic. U.S. Dep. Agric., For. Serv., Washington, DC: Agric. Handb. 618. 29 p.

Falk, J. 1980. Wind damage in spruce-fir stands — literature review with recommendations for harvesting methods. Univ. Maine, Life Sci. Agric. Exp. Sta., Orono, ME: Misc. Rep. 225. 26 p.

Flexner, J.L.; Bassett, J.R.; Montgomery, B.A.; Simmonds, G.A.; Witter, J.A. 1983. Spruce-fir silviculture and the spruce budworm in the Lake States. Univ. Mich. Sch. Nat. Res., Ann Arbor, MI: Handbook 83-2. 30 p.

Frank, R.M. 1979. Methods for modifying stand composition to minimize the impact of spruce budworm infestations. Page 1 *in* Spruce Budworm Proc. Mich. Coop. For. Pest Manage. Progr. Workshop. Escanaba, MI: Vol. 79-1.

Frank, R.M.; Bjorkbom, J.C. 1973. A silvicultural guide for spruce-fir in the Northeast. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Sta., Broomall, PA. Gen. Tech. Rep. NE-6. 29 p.

Frank, R.M.; Blum, B.M. 1978. The selection system of silviculture in spruce-fir stands — procedures, early results, and comparisons with unmanaged stands. U.S. Dep. Agric., For. Serv. Broomall, PA. Res. Pap. NE-425. 15 p.

Ghent, A.W. 1958. Studies of regeneration in forest stands devastated by the spruce budworm. II. Age, height, growth, and related studies of balsam fir seedlings. For. Sci. 4:135-146.

Ghent, A.W.; Fraser, D.A.; Thomas, J.B. 1957. Studies of regeneration in forest stands devastated by the spruce budworm. I. Evidence of trends in forest succession during the first decade following budworm devastation. For. Sci. 3:184-208.

Graham, S.A. 1939. Principles of forest entomology. McGraw-Hall Book Company, Inc., New York.

Graham, S.A.; Orr, L.W. 1940. The spruce budworm in Minnesota. Univ. Minn. Agric. Exp. Sta., Tech. Bull. 142. 27 p.

Greenbank, D.O. 1963a. Host species and the spruce budworm. Pages 219-223 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Greenbank, D.O. 1963b. Staminate flowers and the spruce budworm. Pages 202-218 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Hardy, Y.J.; Lafond, A.; Hamel, L. 1983. The epidemiology of the current spruce budworm outbreak in Quebec. For. Sci. 29:715-725.

Hatcher, R.J. 1964. Spruce budworm damage to balsam fir in immature stands, Quebec. For. Chron. 40:372-383.

Irland, L.C.; Runyon, K.L. 1984. Economics of spruce budworm management strategy. *In* D.M. Schmitt; D.G. Grimble; J.L. Searcy; tech. coords. Managing the Spruce Budworm in Eastern North America. U.S. Dep. Agric., For. Serv., Washington, DC. Agric. Handb. 620.

Jennings, D.T.; Houseweart, M.W. 1984. Predation by eumonid wasps (Hymenoptera: Eumenidae) on spruce budworm (Lepidoptera: Tortricidae) and other lepidopterous larvae in spruce-fir forests in Maine. Ann. Entomol. Soc. Amer. 77:39-45.

Jennings, D.J.; Houseweart, M.W.; Dimond, J.B. 1983. Dispersal losses of early-instar spruce budworm (Lepidoptera: Tortricidae) larvae in strip clearcut and dense spruce-fir forests of Maine. Environ. Entomol. 12:1787-1792.

Kleinschmidt, S.M.; Baskerville, G.L.; Solomon, D.S. 1980. Reduction of volume increment in fir-spruce stands due to defoliation by spruce budworm. Fac. For., Univ. New Brunswick, Fredericton, N.B., Canada. Res. Pap. 37 p.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56:213-221.

MacLean, D.A. 1982. Vulnerability rating of forests in New Brunswick and Nova Scotia to budworm attack. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-132. 21 p.

MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. For. Chron. 60:273-279.

MacLean, D.A. 1985. Effects of spruce budworm outbreaks on forest growth and yield. Pages 148-175 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept. 1984, Bangor, ME. Can. For. Serv. Ottawa, Ont.

McLintock, T.F. 1947. Silvicultural practices for control of spruce budworm. J. For. 45:655-658.

McLintock, T.F. 1948. Evaluation of tree risk in the spruce-fir region of the Northeast. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Sta., Upper Darby, PA. Res. Pap. NE-16. 7 p.

McLintock, T.F. 1954. Factors affecting wind damage in selectively cut stands of spruce and fir in Maine and northern New Hampshire. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Sta., Upper Darby, PA: Res. Pap. NE-70. 17 p.

McLintock, T.F. 1955. How damage to balsam fir develops after a spruce budworm epidemic. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Sta., Upper Darby, PA. Res. Pap. 75.

Montgomery, B.A.; Simmons, G.A.; Witter, J.A.; Flexner, L.J. 1982a. The spruce budworm handbook: A management guide for spruce-fir stands in the Lake States. Mich. Coop. For. Pest Manage. Progr., Ann Arbor, MI. Handbook 82-7. 35 p.

Montgomery, B.A.; Witter, J.A.; Simmons, G.A.; Rogan, R.G. 1982b. The spruce budworm manual for the Lake States. Mich. Coop. For. Pest Manage. Progr., Ann Arbor, MI. Tech. Man. 82-6. 66 p.

Morris, R.F. 1958. A review of the important insects affecting the spruce-fir forest in the Maritime Provinces. For. Chron. 34:159-189.

Morris, R.F.; Bishop, R.L. 1951. A method of rapid forest survey for mapping vulnerability to spruce budworm damage. For. Chron. 27:171-178.

Morris, R.F.; Mott, D.G. 1963. Dispersal and the spruce budworm. Pages 180-189 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Mott, D.G. 1963. The forest and the spruce budworm. Pages 189-202 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Mott, D.G. 1980. Spruce budworm protection management in Maine. Maine For. Rev. 13 (Summer): 26-33.

Mott, D.G.; Nairn, L.D.; Cook, J.A. 1957. Radial growth in forest trees and effects of insect defoliation. For. Sci. 3:286-304.

Piene, H. 1981. Early growth responses to operational spacing in young balsam fir stands on the Cape Breton Highlands, Nova Scotia. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Inf. Rep. M-X-125.

Pistell, A.; Harshberger, D. 1979. The spruce budworm in Maine. A history of forest conditions, forest industry and policy from 1800-1981. Dep. Cons., Maine For. Serv., Augusta, ME.

Prebble, M.L.; Morris, R.F. 1951. Forest entomology in relation to silviculture in Canada. Part III. The spruce budworm problem. For. Chron. 27:14-22.

Redmond, D.R. 1959. Mortality of rootlets in balsam fir defoliated by the spruce budworm. For. Sci. 5:64-69.

Reed, F.L.C., and Associates Ltd. 1978. Forest management in Canada. Vol. 1. Can. For. Serv., Forest Manage. Inst., Ottawa, Ont. Inf. Rep. FMR-X-102.

Royama, T. 1984. Population dynamics of the spruce budworm, *Choristoneura fumiferana* (Clem.). Ecol. Monogr. 54:429-462.

Schmitt, D.M. 1982. Survey of panel discussion on silvicultural approaches to reduce hazard. From the CANUSA-East Working Group Meetings, Oct. 1981. CANUSA Newsletter 21, March 1982.

Sewell, C.D. and J. Maranda. 1978. Problems in salvaging timber affected by the spruce budworm. For. Eng. Res. Inst. Can., Pointe Claire, Que. Tech. Rep. TR-25.

Sewall, James W. Co. 1983. Spruce-fir wood supply/demand analysis. Final Report to Maine Dep. Conserv. James W. Sewall Co., Old Town, ME.

Solomon, D.S. 1983. Changes in growth of spruce-fir stands in the Northeast under varying levels of attack by the spruce budworm. Pages 93-96 *in* Renewable resources inventories for monitoring changes and trends: Proc. Inter. Conf.; August 15-19, 1983. Corvallis, OR: Oregon State University.

Swaine, J.M., and F.C. Craighead. 1924. Studies on the spruce budworm (*Cacoecia fumiferana* Clem.). Part I. A general account of the outbreaks, injury and associated insects. Can. Dep. Agric., Ottawa, Ont. Tech. Bull. 37(n.s.). pp. 3-27.

Turner, K.B. 1952. The relation of mortality of balsam fir, *Abies balsamea* (L.) Mill., caused by the spruce budworm, *Choristoneura fumiferama* (Clem.) to forest composition in the Algoma Forest of Ontario. Can. Dep. Agric., Ottawa, Publ. 875. 107 p.

USDA For. Serv. 1983. Spruce budworm environmental assessment for proposed cooperative spruce budworm integrated pest management program. U.S. Dep. Agric., For. Serv., Northeast. Area, State and Private For. Broomall, PA.

Van Raalte, G.D. 1972. Do I have a budworm-susceptible forest? For. Chron. 48:190-192.

Weetman, G.F. 1982. The evolution and status of Canadian silviculture practice. For. Chron. 58:74-78.

Westveld, M. 1946. Forest management as a means of controlling spruce budworm. J. For. 44:949-953.

Westveld, M. 1953. Ecology and silviculture of the spruce-fir forests of eastern North America. J. For. 51:422-430.

Westveld, M. 1954. A budworm vigor-resistance classification for spruce and balsam fir. J. For. 52:11-24.

Witter, J.A.; Lynch, A.M.; Montgomery, B.A. 1983. Management implications of interaction between the spruce budworm and spruce-fir stands. Pages 127-132 *in* R.L. Talerico, M. Montgomery tech. coords. Forest defoliator — host interaction: a comparison between gypsy moth and spruce budworms: symposium proceedings. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Sta., Broomall, PA. Gen. Tech. Rep. NE-85.

Witter, J.A.; Ostaff, D.; Montgomery, B.A. 1984. Damage assessment. *In* D.M. Schmitt, D.G. Grimble, and J.L. Searcy, tech. coords. Managing the spruce budworm in eastern North America. U.S. Dep. Agric., For. Serv., Washington, DC. Agric. Handb. 620.

Silvicultural Approaches to Western Spruce Budworm Management in the Northern U.S. Rocky Mountains

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Stand susceptibility to western spruce budworm is affected by the interaction of site and stand factors, such as species composition, stand density, height-class structure (tree-height variability), vigor, maturity, site climate, regional climate, and degree of isolation from other susceptible stands. Susceptible stands are primarily shade-tolerant conifers, very dense and of low vigor, multistoried, physiologically mature, and on warm, dry sites characterized by relatively warm, dry regional climate. All factors — except regional and site climate — can be changed silviculturally to reduce susceptibility to budworm. Even-aged management of seral, shade-intolerant species will substantially reduce stand susceptibility; all-aged management is appropriate when nonhost species are featured. Stands can be rated for susceptibility to budworm by using quantitative indexes for important site and stand factors. Silvicultural treatment provides immediate and long-term benefits to treated stands; forest susceptibility will be gradually reduced as more stands are treated. Reducing the habitat of western spruce budworm through silvicultural methods is a good, long-term approach for dealing with budworm in the northern U.S. Rocky Mountains and probably elsewhere in western North America. Silvicultural treatments, however, probably will not be applied extensively in Wilderness or in other lands not designated for timber production. Although our knowledge of budworm has increased substantially during the CANUSA-West Program, much research is needed before we truly understand the interactions between budworm and its environment.

La vulnérabilité d'un peuplement à la tordeuse occidentale de l'épinette dépend de l'interaction de facteurs stationnels et de facteurs liés au peuplement (composition des espèces, densité du peuplement, répartition des classes de hauteur, vigueur, maturité, climats stationnel et régional et degré d'isolement d'autres peuplements vulnérables). Les peuplements vulnérables sont surtout constitués de conifères très denses et peu vigoureux, pluri-étagés et à maturité, qui tolèrent l'ombre et qui occupent des stations chaudes et sèches caractérisées par un climat régional relativement

chaud et sec. Tous les facteurs, sauf les climats régional et stationnel, peuvent être modifiés par des méthodes sylvicoles afin de réduire la vulnérabilité à la tordeuse. L'aménagement de peuplements équiennes d'essences sériales, intolérantes à l'ombre, réduira considérablement leur vulnérabilité; leur aménagement en tous groupes d'âges convient lorsque les essences non hôtes prédominent. La vulnérabilité des peuplements à la tordeuse peut être cotée à l'aide d'indices numériques attribués aux facteurs importants de stations et de peuplements. Le traitement sylvicole procure des avantages immédiats et durables aux peuplements; la vulnérabilité des forêts diminuera graduellement à mesure que davantage de peuplements seront traités. L'amenuisement de l'habitat de la tordeuse occidentale, grâce aux méthodes sylvicoles, est une bonne stratégie à long terme, dans le nord des Rocheuses, aux États-Unis et probablement ailleurs dans l'ouest de l'Amérique du Nord. Toutefois, les traitements sylvicoles ne seront pas utilisés dans la région du "Wilderness" ou les autres non désignées pour la production de bois. Même si nos connaissances de la tordeuse ont augmenté notablement grâce au programme CANUSA-Ouest, beaucoup de travail reste à faire avant que nous ne comprenions vraiment les interactions de l'insecte et de son milieu.

Introduction

The western spruce budworm (*Choristoneura occidentalis* Freeman), a native insect species, is the most widely distributed and destructive defoliator of coniferous forests in western North America (Fellin and Dewey 1982). In the early 1950s, resource managers initiated a series of operational chemical treatment programs — the last in 1966 — to combat the budworm problem. Most programs achieved their goals of local population reduction and these chemical applications reduced defoliation and probably gave some temporary relief to trees and stands.[1] From a broader and long-term perspective, however, our past efforts to manage budworm with insecticides have been unsuccessful; these programs have not "controlled" budworm, changed the course of outbreaks,[2] nor significantly reduced the continuing regional outbreak (Fellin 1980, 1983).

Recently, forest managers and researchers began a major effort in the West to assess the merits of using silviculture to develop a more integrated approach to managing western spruce budworm. The silvicultural approach is appealing because it alters the forest substrate on which budworm depends for survival.

In this paper, we consider silviculture to be "...the theory and practice of controlling the establishment, composition, constitution and growth of forests" (Society of American Foresters 1971). Our purpose is to assess silviculture as an option for managing budworm. We evaluate current research on the relation of budworm to its environment, and we present an array of silvicultural strategies that we believe will reduce stand and forest susceptibility to western spruce budworm.

The Forest, Climate, and Western Spruce Budworm

Forested lands of the northern U.S. Rocky Mountains are ecologically diverse. Principal mountain ranges typically exceed 3 048 m (10,000 ft) MSL (mean sea level) elevation and are frequently dissected by deep valleys, resulting in complex and diverse site conditions that support a wide variety of plant communities (Arno 1979; Daubenmire and Daubenmire 1968; Garrison et al. 1977). Much of the forested land in western North America has been classified according to the potential climax plant community a given parcel will support (Pfister 1981). These classifications — called "habitat types" — collectively and concisely express the wide ecological variation found in the West. Most current field studies in western forests consider habitat types in experimental design, and habitat types have been the basis for much of the current western research on western spruce budworm.

Western spruce budworm has a wide ecological amplitude. Of 64 habitat types identified in Montana

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[1] Terrell, T.T.; Fellin, D.G. 1959. Spruce budworm infestations in the northern Rocky Mountain Region, 1958. U.S. Dep. Agric., For. Serv., For. Insect Lab., Missoula, MT. Unpubl. rep. 10 p.

[2] Terrell, T.T. 1962. Biological evaluations of spruce budworm infestations in controlled areas and proposed control areas in the Northern Region, 1962. U.S. Dep. Agric., For. Serv., Northern Region, Div. State and Priv. For., Missoula, MT. Unpubl. rep. 10 p.

Table 1
Occurrence of western spruce budworm in Montana by forest climax series*

Forest climax series	Elevational range		Mean annual precipitation		Mean July temperature	
	Metres	(Feet)	Centimetres	(Inches)	°C	(°F)
Pseudotsuga menziesii	610-2 377	(2,000-7,800)	43-51	(17-20)	16-19	(60-66)
Picea spp.	884-2 621	(2,900-8,600)	58-66	(23-26)	13-16	(56-61)
Abies grandis, *Thuja plicata*, *Tsuga heterophylla*	610-1 524	(2,000-5,000)	76-86	(30-34)	18	(64)
Abies lasiocarpa (lower subalpine)	975-2 591	(3,200-8,500)	53-135	(21-53)	14-18	(57-64)

*Environmental data taken from Pfister et al. (1977).

(Pfister et al. 1977), 72 percent (46) have been or are now infested. Budworm is common in the warm, dry Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) habitat types found at low elevations and in cool, moist lower subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) habitat types at high elevations (Table 1). Western spruce budworm is seldom found in the limber pine (*Pinus flexilis* James), ponderosa pine (*Pinus ponderosa* Laws.), lodgepole pine (*Pinus contorta* Dougl.), or the upper subalpine fir habitat types (Fellin et al. 1983). Western spruce budworm is commonly found where elevation ranges from 610 to 2 134 m (2,000 to more than 7,000 ft) MSL, average annual precipitation ranges from 43 to 135 cm (17 to 53 inches) per year, and average July temperature ranges from 13 to 19°C (56 to 66° F) (Pfister et al. 1977). Forests within these ranges are common also in central Idaho, (Steele et al. 1981), eastern Idaho – western Wyoming (Steele et al. 1983), and north-central Idaho, and western spruce budworm is frequent there.[3]

Budworm feeding and populations are apparently regulated by various climatic, site, and stand factors. Most of what we know about these factors has been inferred from general principles and is not backed by data derived experimentally — but we believe these inferences are generally true.

Regulating factors interact to influence budworm populations and damage — that is, stand *susceptibility* and *vulnerability* to budworm. Mott (1963) defines susceptibility as the probability that a stand will be infested, and vulnerability as the probability that damage to trees and stands will result, given an infestation.

Knowledge of the effects of climatic, site, and stand factors on the western spruce budworm is essential to develop silvicultural strategies that will reduce stand and forest susceptibility. Carlson et al. (1983), and Wulf and Cates (in press) comprehensively reviewed relations between western spruce budworm and coniferous forests. Here, we briefly discuss the eight most influential climatic, site, and stand factors; regional climate, intrinsic site climate, species composition, host/nonhost density, stand structure (vertical and horizontal), stand vigor, stand maturity, and continuity of surrounding host type.

Regional Climate

Outbreaks of western spruce budworm are generally associated with drier climates where annual precipitation ranges from 23 to 91 cm (9 to 36 inches).[4] Outbreaks seldom occur west of the Cascades in Washington and Oregon, nor in extreme northern Idaho and northwestern Montana where the climate is best characterized as neo-coastal (Arno 1979), even though stands in those areas would otherwise appear to be susceptible. This climatic relation also applies to high-elevation stands that are usually very moist. Cold temperatures may interact with the very moist conditions to further reduce susceptibility in stands above 2 000 m (6,500 ft). Outbreaks are much more frequent in the inland forests with drier climates (see footnote 4); within the drier areas, defoliation tends to increase when mean temperatures increase and precipitation decreases, in the year preceding defoliation (Twardus 1980).[5]

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[3] Cooper, S.; Neiman, K. ; Steele, R. 1983. Review draft: forest habitat types of northern Idaho. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT, and Region 1, Missoula, MT. 210 p.

[4] Kemp, W.P. 1983.The influence of climate, phenology, and soils on western spruce budworm defoliation. Ph.D. Dissertation, Univ. Idaho, Moscow, ID. 143 p.

How climate affects feeding and other activities of western spruce budworm is largely unknown, but host stress has been postulated as a cause. For example, larval survival was higher and females were 30-percent heavier when Douglas-fir stands were water stressed (Cates et al. 1983). Increased susceptibility may result from a decrease in resistance compounds found in the trees; bornyl acetate and beta-pinene were significantly lower in stressed trees. Laboratory studies indicated budworm growth rates were higher when nitrogen and beta pinene were increased in the artificial medium but growth rates decreased when bornyl acetate increased.[6] The role of beta-pinene apparently reversed in the laboratory study, but the roles of nitrogen and bornyl acetate were consistent.

Even though the work on foliar chemistry (Cates et al. 1983, see footnote 6) shows terpenes and nitrogen in drought-stressed trees favor budworm survival and development, other climatic factors acting directly on the insect but not yet adequately studied may be equally or more important. For example, larval development on artificial medium was enhanced under constant warm, dry conditions (20°C), but was retarded when temperature fluctuated about a mean of 20°C.[7] Thus, cool fluctuating temperatures probably extend the period of larval development, predisposing larvae to more predation; bacterial, fungal, and viral diseases also may be more prevalent under cool, moist conditions. Furthermore, short-term weather events may dramatically affect budworm; populations were reduced up to 90 percent in Montana after unseasonable spring frosts (Fellin and Schmidt 1973a).

Site Climate

Site climate may be defined as regional climate modified by the interaction of slope, aspect, elevation, and physiography at a given location. Susceptibility to western spruce budworm is greatest in stands on dry, warm sites with shallow soils (Carlson and Theroux 1982; Despain 1981; Fauss and Pierce 1969; Fellin 1980; Sutherland 1983),[8] if the general regional climate is conducive to budworm. Warm and dry sites also favor other closely related budworm species (Blais 1958; Shepherd 1959). Conversely, cool, moist sites are much less favorable. Reasons for improved budworm success on warm, dry sites are probably similar to those discussed for warm, dry regional climate. Decreased defensive chemistry occurs in trees in some moisture-stressed sites, and this altered chemistry may be a general phenomenon at other stressed sites regardless of the types of terpenes that confer resistance to budworm (Cates et al. 1983, see footnote 6). Also, warm temperatures tend to increase the rate of larval development (Wagg 1958), and tree crowns on southwestern dry exposures would be warmer than those on northern exposures for a given elevation. Thus, budworm survival and health are probably better on warm, dry sites — as has been shown for spruce budworm in eastern North America (Mott 1963; Wellington 1949).

Nutrient stress may increase stand susceptibility. Hypothetically, warm, dry microsites tend to support increased litter decomposition and humus mineralization, and may cause plant nutrient deficiencies. Increased decomposition of organic matter also may increase the acidity of the soil, which may alter the cycling of ions important to plant growth and development (see footnote 8).

Stand Composition

Stand composition, which directly affects susceptibility to western spruce budworm, includes:

- the number of different species and the proportion of each in the stand;
- the successional status of the stand; and
- genetic variation in the host species.

Species Composition

Many western conifer species are budworm hosts (Fellin et al. 1983). Douglas-fir, grand fir, subalpine fir, white fir (*Abies concolor* (Gord. & Glend.) Lindl.), Engelmann spruce (*Picea engelmannii* Parry), and western larch are the primary food of western spruce budworm. Ponderosa pine, lodgepole pine, and others not used primarily as food can serve as overwintering niches for the larvae. For simplicity, we consider species that contribute substantially to the diet as "host" and those that do not as "nonhost" — although we recognize that nonhost species can be important in the dynamics of budworm.

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[5] Hard, J.; Tunnock, S.; Eder, R. 1980. Western spruce budworm defoliation trend relative to weather in the Northern Region, 1969-1979. U.S. Dep. Agric., For. Serv., Div. State and Priv. For., For. Insect and Dis. Manage., Missoula, MT. Unpubl. Rep. 80-4. 10 p.

[6] Cates, R.G.; Henderson, C.B.; Redak, R.A. 1983. A determination of the effect of nitrogen and terpenes on spruce budworm growth and survival. Univ. New Mexico, Albuquerque, NM. Final rep. to Canada/United States Spruce Budworms Program West. 25 p.

[7] Beckwith, R.C. 1983. Effects of laboratory temperatures on the western spruce budworm. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., La Grande, OR. Prog. rep. 9 p.

[8] Stoszek, K.J.; Mika, P.G. 1983. The relationships of western spruce budworm outbreaks to site/stand attributes, development and management history: model completion and comparison. Univ. Idaho, Moscow, ID. Final rep. to CANUSA-West Spruce Budworms Program. 70 p.

Stand susceptibility and vulnerability increase as the proportion of hosts increases (Carlson and Theroux 1982; Fauss and Pierce 1969; see footnote 8). Highly diverse stands with several tree species tend to be least susceptible and vulnerable (Carlson et al. 1983; Schmidt et al. 1983).

Successional Status

The proportion and age distribution of shade-tolerant conifer species determine the successional status of a stand (Daubenmire and Daubenmire 1968) and, consequently, the susceptibility of the stand to western spruce budworm. Generally, the most shade-tolerant conifers are the most susceptible; stands with a high proportion of shade-tolerant species tend to be near climax and highly susceptible. Host species ranked least to most shade tolerant are also ranked least to most in susceptibility to western spruce budworm: western larch, Douglas-fir, Engelmann spruce, white fir, grand fir, and subalpine fir.

The relation of shade tolerance to susceptibility varies among habitat types. Generally, the indicated climax conifer is the most shade tolerant and the most prone to infestation by budworm. When a host species is not the indicated climax, it is relatively less shade tolerant and less susceptible than the climax host species. For example, on Douglas-fir habitat types, Douglas-fir is more shade tolerant than its associates and very susceptible to budworm. Other species — ponderosa pine, lodgepole pine, and western larch — are less tolerant and far less susceptible. On grand fir habitat types, grand fir is highly susceptible, but Douglas-fir is relatively shade intolerant and much less susceptible (Sutherland 1983). We have commonly observed, where grand fir and Douglas-fir of the same size and dominance are growing side by side, very heavy defoliation on grand fir but barely noticeable defoliation on the Douglas-fir. This difference in defoliation also has been observed by others (Carolin and Coulter 1975; Williams 1966, 1967).[9] Furthermore, larval densities were found to be higher on subalpine fir than on Douglas-fir, in a subalpine fir habitat type (Williams et al. 1971).

Reasons for the influence of shade tolerance on susceptibility and vulnerability are unknown and have not been investigated. Asynchrony between budburst and spring larval feeding might be a cause. On grand fir habitats, buds of shade-tolerant grand fir burst earlier than on associated Douglas-fir, and would thus be an earlier source of food to emerging larvae. But because larval dispersal is passive — the small larvae can be moved by wind — the insects should be evenly distributed among species at the beginning of the feeding period. As the larvae emerge from hibernacula in the spring, they may sense aromatic compounds emitted by flushing buds of true firs. Larvae on grand and subalpine firs would tend to stay there, but larvae on Douglas-fir may actively search for the source of the stimulant and leave the trees. Terpenes may be important in this hypothetical process; beta-pinene has been shown to be a feeding stimulant for budworm (see footnote 6). In Douglas-fir habitats, the terpene gradient between hosts would be less, and thus the searching activity of larvae would be minimized.

Genetic Variation

Susceptibility of western conifer forests to budworm is also influenced by intraspecific genetic variability — another aspect of stand composition. Apparent phenotypic resistance to feeding has been observed in the northern U.S. Rocky Mountains (Cates et al. 1983; McDonald 1979, 1981); feeding behavior of the larvae is apparently related to inherited factors in Douglas-fir. Willhite and Stock (1983) suggest that genetically different populations occur in western Montana and northern Idaho, but the differences are independent of host or environmental variation. Further work by McDonald (in press) suggests that resistance of Douglas-fir to budworm feeding has a 0.42 heritability and that significant genetic gains could be made through intensive breeding. McDonald's work apparently supports the conclusions of Willhite and Stock. Variations in the chemistry of toxic natural products investigated by Cates et al. (1983) undoubtedly have a strong genetic basis. No breeding experiments have yet led to the development of budworm-resistant trees.

Stand Density

Stand density likely influences susceptibility to western spruce budworm. As density of host species increases, susceptibility apparently also increases (Carlson et al. 1983; Despain 1981; Fauss and Pierce 1969; Wulf and Cates, in press). Dispersing budworm larvae are less likely to reach suitable substrate in open than in dense stands, and larvae that fall to the ground likely starve or are eaten by predators.

Recent studies generally show that the number of dispersing larvae is not related to stand density. Density of early instars collected 0.5 m (1.5 ft) above the ground were not different between 6-ha (15-acre) clearcut, selection, overstory-removal, or understory-removal cuts — and no edge effect was found in any of the cutting units at Lubrecht Experimental Forest in an infestation of western spruce budworm.[10] At Newman

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[9] Mika, P.; Twardus, D. 1983. Western spruce budworm impact assessment: hazard model validation and vulnerability model development. Univ. Idaho, Moscow, ID. Prog. rep. to CANUSA-West Spruce Budworms Program. 39 p.

[10] Fellin, D.G. 1981. Dispersal of stage II western spruce budworm larvae and flight behavior and dispersal of adults as related to stand conditions and silvicultural practices. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Missoula, MT. Final prog. rep. for the period 1 April-30 September 1980. 57 p.

Ridge where budworm populations were low, a significant edge effect was found in only one of four 12-ha (30-acre) clearcut units (see footnote 10). In another study in western Montana, early-instar catches were essentially random and showed no relation to residual stand density.[11] Fellin (unpublished observation) reported one site, however, where larval densities were significantly lower in clearcut than in the adjacent uncut stand. Considered collectively these studies indicate that early instars may be dispersed more or less uniformly and that this dispersal is independent of the density of individual stands in the area. Beckwith and Burnell (1982) speculate that turbulent air currents could account for higher catches of budworm larvae at higher crown levels; if so, considering the turbulent winds that occur in the northern Rockies, an even redistribution of larvae may be expected during spring dispersal within an area of infestation.

Recent research[12] supports the suspected direct relation of stand density to budworm susceptibility. Thinning an overstocked Douglas-fir stand to a spacing of 4.3 × 4.3 m (14 × 14 ft) significantly reduced defoliation (an index of susceptibility) and accelerated the radial growth of the leave trees.

Number of adult budworm moths may be a good index to stand susceptibility, and dispersal behavior of adult males is directly related to stand density. In field studies in western Montana (see footnote 10), increasing numbers of males were caught as stand density increased. We presume, because the males are attracted to the females, that the number of adult females also would increase with stand density, supporting the contention that susceptibility increases with increasing stand density.

Stand Height-Class Structure

Height-class structure (tree-height variability) significantly influences stand susceptibility to western spruce budworm. In multistoried, uneven-aged stands where the intermediate canopies are host species, larvae are more likely to land on suitable substrate where they can feed and develop (Johnson and Denton 1975).

Increasing variation in age, height, and diameter indicates an uneven-aged, multistoried stand structure (see footnote 8). Average defoliation increased as the variation in height, diameter, and age increased in subalpine fir habitats; the opposite effect was found in the western hemlock forest climax series (see footnote 8). Small trees are damaged more than large trees in two-storied stands (see footnote 9), and one-storied seral stands appear to be least susceptible (see footnote 11).[13]

Uneven-aged stands may provide a more favorable microclimate for larval development. Increasing exposure to sunlight has been found to favor development of spruce budworm larvae in conifer forests of the eastern United States (Mott 1963; Wellington 1949). Western spruce budworm larval development is hastened by warm temperatures (Wagg 1958), and a greater proportion of the crowns of dominant and codominant trees are exposed to direct sunlight in uneven-aged stands.

Tree and Stand Vigor

Vigorous trees probably are less susceptible to western spruce budworm than trees under stress (see footnote 12; Williams 1966, 1967). Cates and his coworkers (1983) reared budworm on both water-stressed and vigorous nonstressed trees and found larval survival was 69 percent greater and adults were 20 to 30 percent heavier on the stressed trees. They also found an increase in development and survival rates when budworm were reared on trees with declining radial increments. In Idaho, tree defoliation was positively correlated with basal-area increment, but the study trees had a declining growth rate and may have been less vigorous (see footnote 8).

Vigorous trees — those growing rapidly — usually have more fully developed crowns than slower growing individuals. At a given larval density, the vigorous tree would have a lower density of larvae per unit of foliage biomass, probably resulting in lower percent defoliation — and less effect on net fiber production. The vigorous tree could better withstand repeated defoliation because its carbohydrate resources would remain higher. The combination of increased carbohydrate, decreased budworm density per biomass unit, and an increase in chemical deterrents (Cates et al. 1983) — along with other variables not yet studied — all may contribute to decreased susceptibility and vulnerability of vigorous trees.

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[11] Carlson, C.E.; Theroux, L.J.; McCaughey, W.W. 1982. The influence of silvicultural practices on the susceptibility and vulnerability of northern Rocky Mountain forests to the western spruce budworm. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Missoula, MT. Comprehensive prog. rep. for 1 April 1981-31 March 1982. 55 p.

[12] Carlson, C.E.; Pfister, R.D.; Theroux, L.J.; Fiedler, C. 1984. Influence of thinning second-growth Douglas-fir on feeding activity of western spruce budworm. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Manuscript in preparation.

[13] Scott, D.R.M.; Nichols, T. 1983. Growth impacts on host trees due to western spruce budworm defoliation on the east slope of the Washington Cascades. Univ. Wash., Seattle, WA. Final rep. to CANUSA Spruce Budworms Program-West. 71 p.

Maturity of Trees and Stands

Susceptibility of trees and stands to western spruce budworm usually increases as stands mature. Small, young trees regenerated through even-aged cutting methods are only slightly susceptible (Carlson et al. 1983). Adult moths tend not to lay eggs on small trees, which are also poor targets for spring-dispersing larvae. Larvae that do land on small trees are in danger of being eaten by ants, birds, spiders, and other predators (Campbell et al. 1984).[14]

Young western larch, although not very susceptible, can be damaged by budworm. Few larvae may be found on any given tree, but they tend to mine and sever the growing shoots, cause forked and bushy tops, and reduce net height growth by 25 to 30 percent in the tops of affected trees (Fellin and Schmidt 1967, 1973b; Schmidt and Fellin 1973). Terminal damage may be temporary, however, because larch exhibits strong apical dominance and the laterals adjacent to the terminal shoot soon take over and regain most of the lost height growth (Fellin and Schmidt 1973b). In an extensive study of over 150 stands in western Montana, only 10 percent of the young larch sampled had terminal shoots severed by budworm during the previous 5 years (Carlson et al. 1983), although populations were high in adjacent stands. Sustained feeding in young larch stands, however, results in significant damage to growing stock.

Curiously — based on limited observations — older and larger western larch (50 to 60 years, 20 m (65 ft) high) sustain little budworm damage to growing shoots.[15] Several western larch growing with crowns interlaced with adjacent, heavily defoliated Douglas-fir were fed on only slightly by budworm. Elsewhere, however, we noticed that budworm fed substantially on mature larch.

Susceptibility may be related to sexual maturity. As trees and stands mature, flowering increases. Young pollen and seed cones break buds earlier and are thought to be more nutritious than vegetative buds (Wulf and Cates, in press). Second instars are frequently found in immature pollen and seed cones, and can be responsible for significant depletion of seed crops (Chrisman et al. 1983).[16]

As reported for spruce budworm in the eastern United States, flowering is a symptom of the aging process and susceptibility to budworm may be more related to the maturity of the tree or stand than to flower production (Greenbank 1963). As a tree ages, it becomes larger and produces more substrate for feeding larvae; becomes more suitable for egg deposition; produces flowers, which afford early habitat for small, feeding larvae; becomes less accessible to predators — especially ants; and may be a biochemically better substrate for budworm.

Continuity of Host Type

As the acreage of susceptible host type increases, the susceptibility of stands within or adjacent to that host type is assumed to increase (Carlson et al. 1983). Large acreages of mature budworm-infested forest may produce large quantities of budworms. Wind-dispersed larvae are probably transported to nearby stands; few data are available on just how far first and second instars can be carried. The distance small larva, buoyant on silken threads, could be carried is likely a function of wind velocity and turbulence during dispersal.

Adult budworm in the northern Rocky Mountains are believed to move only short distances from the stands in which they pupated. They tend to search for oviposition sites in or near their home areas. A mass movement of adults from a forested area to a sterile city environment has been observed, however (Johnson and Denton 1975). Recent studies on population dynamics suggest indirectly that adults may at times move significant distances — how far is not known (Campbell, in press). Even though mass migrations of adult spruce budworms occur often in the eastern United States and eastern Canada, the unique topography and wind patterns of the western United States and Canada probably limit mass movements of adults, but the issue of how far western spruce budworm adults disperse remains unresolved.

Historical Events Contributing to Forest Susceptibility

Little is known of the extent and duration of western spruce budworm before the early 1900s. According to Johnson and Denton (1975), the first outbreak in western Canada was reported in 1909 and in the western United States in 1922. Western spruce budworm is native and outbreak populations likely caused defoliation, loss of radial and height growth, and mortality of host trees from time to time before 1900.

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[14] Carlson, C.E.; Campbell, R.W.; Theroux, L.J.; Egan, T.H. 1984. Ants and birds reduce western spruce budworm feeding injury to small Douglas-fir and western larch in Montana. Editorial draft submitted to For. Ecol. and Manage.

[15] Carlson, C.E.; Fellin, D.G. 1983. Personal observations concerning western spruce budworm feeding behavior in second-growth western larch at Lubrecht Experimental Forest in western Montana. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., For. Sciences Lab., Missoula, MT.

[16] Shearer, R.C.; Tiernan, C.J. 1981. Effects of western spruce budworm on cone and seed production, northern Rocky Mountains. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Missoula, MT. Comprehensive prog. rep. for 1 April 1980-31 March 1981. 54 p.

With our knowledge of the factors affecting budworm population dynamics — albeit incomplete — we speculate that forest conditions have become much more favorable for the insect since intensive forest fire prevention and suppression policies and selective logging practices were invoked in the early 1900s. In Douglas-fir habitats of western Montana, average fire-free intervals before the 1900s for a given site were only 15 to 30 years; maximum intervals were 35 to 60 years (Arno 1980). These frequent fires often destroyed shade-tolerant understory conifers and thinned out some of the larger trees. Reduced fire frequency has allowed shade-tolerant, budworm-susceptible conifers to become established in significant numbers (Dickman 1978; Gruell et al. 1982). As a result, multistoried, uneven-aged forests have developed that are now highly susceptible to western spruce budworm.

Past forest management also has encouraged the development of susceptible forests. "Loggers choice" selective harvesting often extracted the best timber, leaving the stressed, often shade-tolerant conifers (Schmidt et al. 1983). These low-vigor leftovers — protected from fire — survived and now occupy many of the good growing sites (Figure 1). Past fire-management policies, combined with selective harvesting practices, have increased forest and stand susceptibility by:

- increasing the biomass of shade-tolerant conifers;
- maintaining low-vigor trees;
- creating multistoried canopies;
- increasing stand density and, therefore, moisture stress in the stand;
- increasing the proportion of host to nonhost; and
- increasing the continuity of surrounding host type.

Silvicultural Treatment to Reduce Stand Susceptibility and Vulnerability

Many of the factors believed to influence stand susceptibility to western spruce budworm — species composition, relative density of host and nonhost, height structure, vigor, age, and character of the surrounding forest — can be changed through silvicultural activities and probability of infestation can be reduced (Carlson et al., in press b). Forests are composed of mosaics of stands ranging from low to high susceptibility. Other concerns being equal, highly susceptible stands should be treated before stands of lesser susceptibility. If stands are to be treated silviculturally to reduce probability of infestation by budworm, a method is needed to rank stands for susceptibility. Treatment priorities then can be set, and managers can prescribe appropriate treatments. We discuss our method for rating stand susceptibility, suggest treatment strategies for mature and immature stands, and speculate on the effectiveness of the silvicultural approach.

Rating Stand Susceptibility

In rating susceptibility or hazard to the western spruce budworm, the entire stand or forest must be considered. We have defined host trees as those on which the larvae feed, but because of the effect of various site and stand factors on the relation of the forest to budworm (see the Forest, Climate, and Western Spruce Budworm section) we must consider all species — host and nonhost — in evaluating stand susceptibility.

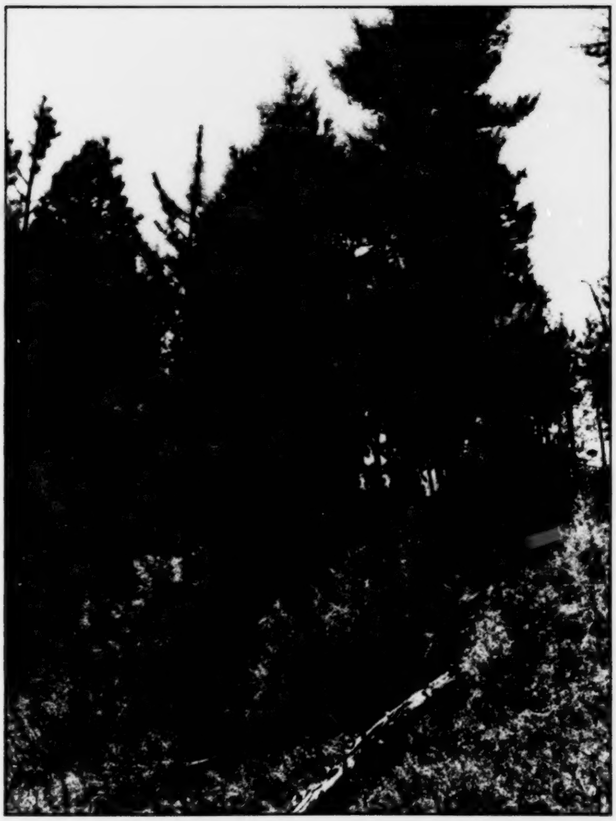

Figure 1. Selective logging of pine and effective fire prevention since the early 1900s resulted in this low-vigor stand of Douglas-fir, now highly susceptible to western spruce budworm. The stand is near the climax stage of succession and the shade-tolerant Douglas-fir regeneration has been extensively defoliated, similar to the overstory.

Three different methods have recently been proposed to rate stand susceptibility or hazard to western spruce budworm. One by Heller and Anderson,[17] is based on interpretation of aerial photographs; another by Stoszek and Mika, is based on field data (see footnote 8); and the third is based on interpretation of published and unpublished research on budworm in eastern and western North America (Wulf and Carlson, in press). The first two methods are regression models in which percentage of defoliation of host trees is the dependent variable, and several site and stand variables are independent variables. The models predict defoliation of host trees given certain site and stand conditions — that is, they are models of host-tree vulnerability. The models of Stoszek and Mika (see footnote 8) and Heller and Anderson (see footnote 17) were developed from data collected on the Clearwater and Payette National Forests in Idaho and are applicable only to those locations.

Wulf and Carlson's method (in press) brings together all the factors believed to influence whole-stand susceptibility and derives a single index number to represent relative susceptibility. The model appears to be applicable to conifer forests over most of the northern U.S. Rocky Mountains. Factors, variables, and index values in the model are listed in Table 2. Index values assigned to classes of each variable are multiplied over all factors for a given stand. The product, or stand-susceptibility index, varies from 0 to 100, and stands can be ranked by the index for susceptibility to budworm. Susceptibility indexes of 0 to 20 indicate low hazard, 21 to 50 are moderate, and 50+ are high. As examples, susceptibility indexes have been calculated for a slightly susceptible stand (A), and a stand (B) that is moderately susceptible (Table 3). The susceptibility index (SUIN) is derived as follows:

Stand A

$$\text{SUIN} = \overset{a}{0.3} * \overset{b}{0.6} * \overset{c}{1.3} * \overset{d}{1.1} * \overset{e}{1.1} * \overset{f}{1.1} * \overset{g}{1.0} * \overset{h}{1.0} * \overset{i}{1.2} = 0.37$$

Stand B

$$\text{SUIN} = \overset{a}{1.8} * \overset{b}{2.0} * \overset{c}{1.5} * \overset{d}{1.6} * \overset{e}{1.2} * \overset{f}{1.7} * \overset{g}{1.3} * \overset{h}{1.2} * \overset{i}{1.7} = 47$$

where a = index for percent host crown cover;
b = index for percent climax host crown cover;
c = index for percent crown cover of all species;
d = index for relative stand density;
e = index for mean host age;
f = index for coefficient of variation of height-structure;
g = index for habitat type;
h = index for National Forest; and
i = index for percent host type in surrounding forest.

Table 2
Factors, variables, and indexes used in the hazard model (Wulf and Carlson, in press)

1. Species composition

A. Variable: Percent host crown cover $= \frac{\text{host crown cover}}{\text{total crown cover}} \times 100.$

Hosts considered are Douglas-fir (DF), grand fir (GF), subalpine fir (SAF), white fir (WF), Engelmann spruce (ES), and western larch (WL).

Percent host crown cover	Index value
1-10	0.1
11-20	0.3
21-30	0.5
31-40	0.8
41-50	1.0
51-60	1.3
61-70	1.6
71-80	1.8
81-90	2.1
91-100	2.4

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[17] Heller, R.C.; Anderson, H.N. 1981. The use of photo interpretation and remote sensing techniques to establish hazard rating criteria for spruce budworm susceptible stands. U.S. Dep. Agric., For. Serv., CANUSA Spruce Budworms Program-West, Portland, OR. CANUSA-West final rep. 48 p.

Table 2 **(cont'd)**

B. Variable: Percent climax host crown cover $= \dfrac{\text{climax host crown cover}}{\text{total crown cover}} \times 100.$

Climax hosts considered are DF, GF, WF, SAF, and ES — depending on the habitat type. Only the major climax host species indicated for the habitat type is used, except within the GF and ES series, which include SAF when it is a minor climax species.

Percent host crown cover	Index value
1-10	0.6
11-20	1.0
21-30	1.3
31-40	1.6
41-50	1.8
51-60	2.0
61-70	2.1
71-80	2.2
81-90	2.3
91-100	2.4

2. Density

Variable: Total percent crown cover (all tree species).

Percent crown cover	Index value
1-20	0.8
21-40	1.1
41-60	1.3
61-80	1.4
81-100	1.5
100+	1.6

3. Height-class structure

Variable: Coefficient of variation of host (climax and seral) tree heights. Hosts considered are DF, GF, WF, SAF, ES, and WL.

0-10	0.9
11-20	1.1
21-30	1.3
31-40	1.5
41+	1.7

4. Vigor

Variable: Relative stand density (with or without host-tree biotic stress) $= \dfrac{\text{total basal area}}{\text{average maximum basal area}} \times 100.$

All tree species are used to calculate total stand basal area. The average maximum basal area for the stand is derived from the stocking level assessments of Forest Inventory data and is specific to subregion, habitat-type group, and quadratic mean stand diameter. In addition, the host species (DG, GF, WF, ES, SAF, and WL) are considered stressed by biological agents if more than 30 percent of the host trees are infected with diseases or infested by insects that do not use or destroy budworm food (new foliage).

Table 2 **(cont'd)**

Relative stand density	Index values	
	Without biotic stress	With biotic stress
1-40	0.9	1.0
41-60	1.1	1.2
61-80	1.3	1.4
81 +	1.5	1.6

5. Maturity

Variable: Basal-area-weighted mean host age. Hosts considered are DF, GF, WF, SAF, and ES. WL is purposely not included because older larch are only slightly susceptible.

Mean host age	Index value
1-25	0.3
26-50	1.0
51-75	1.1
76-150	1.2
150 +	1.3

6. Site climate

Variable: Habitat-type group or potential climax plant community.

Habitat group	Index value
Cold subalpine fir, timberline types	0
Cool, moist spruce; cool, moist subalpine fir types	0.6
Warm, wet grand fir; western redcedar; western hemlock; warm, wet subalpine fir types	1.0
Cold Douglas-fir; cold grand fir; cool, dry spruce; cool, dry subalpine fir types	1.2
Moist grand fir; warm, moist spruce types	1.3
Mesic Douglas-fir; dry grand fir; warm mesic spruce; warm, dry subalpine fir types	1.4
Warm, dry Douglas-fir types	1.5

7. Regional climate

Variable: National Forest or Forest Service Region location with respect to maritime climatic influences. (Interior British Columbia would probably have an index value of 1.0 or 1.1.)

National Forest or Region	Index value
R-6 (west of the Cascades)	0
Idaho Panhandle (exclusive of the St. Joe), Kootenai	0.2
St. Joe, Clearwater, Lolo (westside), Nezperce (Selway District only), Colville	1.0

Table 2 **(concluded)**

Flathead, Nezperce (exclusive of the Selway District), Wallowa-Whitman, Umatilla, Malheur, Ochoco, Okanogan, Wenatchee, Boise, Payette	1.1
Bitterroot, Lolo (eastside), Beaverhead, Custer, Deerlodge, Gallatin, Helena, Lewis and Clark, R-4 (exclusive of the Boise and Payette), R-2, R-3	1.2

8. Surrounding host-type continuity

Variable: The percent host type of the surrounding 400 ha (1,000 acres) and the preponderance of host-type stands immediately adjacent to the subject stand.

Stands are considered "host type" if they are dominated by primary host species (GF, WF, DF, SAF, ES). Even-aged regeneration stands and stands occupying the cold subalpine fir series are not considered host type regardless of their species composition.

Percent host type in the surrounding 400 ha (1,000 acres)	Character of adjacent stands	Index value
0-15	nonhost	0.6
0-15	host	0.8
16-25	nonhost	1.0
16-25	host	1.2
26-75	nonhost	1.4
26-75	host	1.5
76-100	nonhost	1.6
76-100	host	1.7

Table 3

Hazard ratings of two hypothetical stands: A, slightly susceptible to budworm; B, moderately susceptible

		Stand A		Stand B	
Factor	Criterion variable	Actual value	Index value	Actual value	Index value
Composition	A. Percent host crown cover	15	0.3	72	1.8
	B. Percent climax host crown cover	5	0.6	54	2.0
Density	Percent crown cover	54	1.3	95	1.5
Vigor	Relative stand density	44	1.1	84	1.6
Maturity	Mean host age	54	1.1	115	1.2
Height structure	Coefficient of variation	15	1.1	65	1.7
Site climate	Habitat type group	Moist subalpine fir	1.0	Warm Douglas-fir	1.3
Regional climate	National Forest	Clearwater	1.0	Helena	1.2
Surrounding forest	Percent host in surrounding 400 ha (1,000 acres)	22	1.2	78	1.7

Values for each variable can be obtained from the Timber Stand Management Record System, such as the one used by the USDA Forest Service Northern Region, to simplify the process of ranking large numbers of stands. The strength of this interpretive model is its reflection of the biology of the western spruce budworm and its performance during preliminary field tests. Foresters understand the input variables because they are used in everyday resource work. Undoubtedly, the model will need fine-tuning as new information is developed. Nevertheless, the model serves now as a strong working hypothesis for western spruce budworm dynamics and has pragmatic applicability.

Treatments for Mature Stands

Even-aged and uneven-aged regeneration cutting methods can be used in mature stands to alter stand factors and reduce susceptibility to western spruce budworm (Carlson, in press b). Generally, practices that are inherently "good silviculture" also strongly discriminate against budworm. Salvage of trees killed by budworm or removal of vulnerable living trees (presalvage) may also reduce losses to the insect.

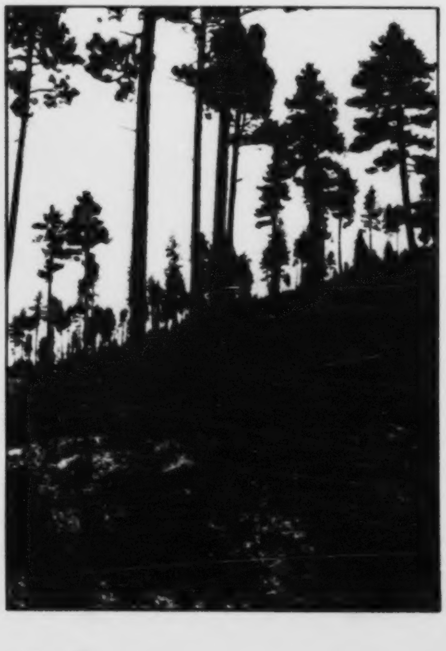
Even-Aged Methods

Even-aged harvest methods currently used in the western United States include clearcut, seed-tree, and shelterwood (Figure 2). Although differing in the amount of overwood left at harvest, each method results in an even-aged stand of regeneration, usually composed largely of seral species (Smith 1962). Even-aged methods are particularly effective in altering the factors influencing stand susceptibility to budworm, and they immediately reduce the quantity and quality of budworm habitat (Carlson et al. 1983; see footnote 8). Species composition is changed and seral conifers with low susceptibility to budworm can be favored. Stand density (residual stand) is reduced, increasing larval losses during dispersal and reducing the numbers of sites for egg deposition. Tree vigor likely is enhanced, possibly strengthening the natural defensive chemistry of residual host trees (Cates et al. 1983). Furthermore, variation in crown height within the residual stand, such as in a shelterwood, is substantially reduced by even-aged harvest methods, contributing to losses during larval dispersal. Even-aged methods also break the continuity of host type.

Uneven-Aged Methods

Uneven-aged methods, as practiced in the past, have led to forests highly susceptible to western spruce budworm in the western United States (Schmidt et al. 1983). Selective harvesting — in which only the best trees were taken (usually the residual old-growth seral species) — coupled with fire exclusion and inadequate site preparation, encouraged the development of multistoried, dense forests dominated by shade-tolerant species. These past practices have caused uneven-aged methods to be held in disfavor for budworm management. In some circumstances, however, uneven-aged management is warranted and will reduce susceptibility to budworm. For example, in dry Douglas-fir habitat types where ponderosa pine is a seral nonhost, the pine can be perpetuated in an uneven-aged condition with group selection cutting augmented with prescribed underburning: the shade-tolerant, bud-

Figure 2. Even-aged methods, such as clearcutting (top) and seed-tree cutting (right) result in even-aged stands composed primarily of seral conifer species. These species and stands have low susceptibility to western spruce budworm.



worm-susceptible Douglas-fir that become established through natural processes can be nearly eliminated through judicious use of light ground-fire. These light fires kill the firs and prepare seedbeds for the pine, essentially creating conditions existing before European settlement of the West.[18]

Uneven-aged management has been recommended by Stoszek and Mika (see footnote 8) to reduce budworm impact in the western hemlock and the subalpine fir climax forest series of northern Idaho. They found heaviest defoliation in young, free-growing *Abies* stands on western hemlock habitat types; vertically diverse stands were least affected, suggesting that uneven-aged management may reduce vulnerability to budworm. Stoszek and Mika (see footnote 8) used regression techniques to draw inferences about the relation of defoliation to site and stand characteristics. Variables and coefficients were found to be substantially different between areas, and separating cause and effect was difficult. Using the hypothetical "discoupled ion theory" of Ulrich (1983), Stoszek and Mika hypothesize: soil nutrient deficiencies are the primary cause of budworm outbreaks in their study area, even-aged management will further aggravate the problem through changes in basic soil chemistry, and all-aged management may be beneficial. Recent work by Stark (1979) and DeByle and Packer (1981), supported by their extensive field data on soils chemistry, suggests soils are little changed by even-aged management in the northern Rocky Mountains. Thus, whether nutrient stress in managed stands influences susceptibility to budworm remains unanswered.

Treatments for Immature Stands

We define immature stands as those not developed to the replacement point. Immature stands can be conveniently divided into seedling and sapling stands, and pole stands.

Seedling and Sapling Stands

Young, even-aged conifer stands are poor habitat for budworm. Generally, these stands are composed of seral species not preferred by the insect. The small trees, often less than 4.6 m (15 ft) tall, have a relatively small foliar biomass and are poor targets for larvae dispersing in spring and late summer. The host trees often are vigorous, fast-growing, and likely possess strong defensive chemistry. Larvae that do land on a host are still vulnerable — up to 50 percent of the population can be lost to predation (Campbell et al. 1984; see footnote 14). Furthermore, larvae dispersing from small trees are likely to fall to the ground and perish.

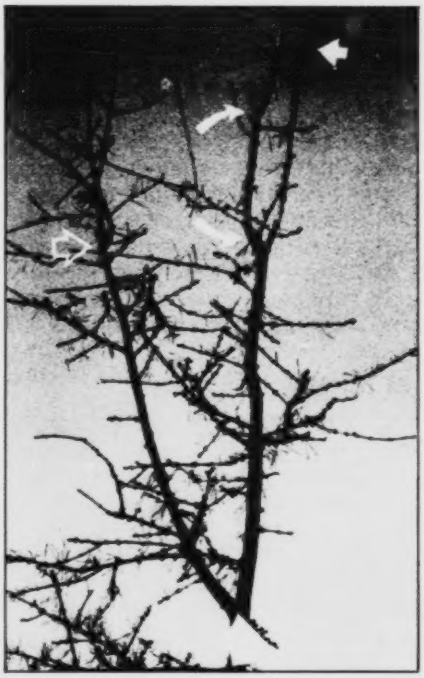


Figure 3. Western spruce budworm often sever the terminal and lateral shoots (arrows) of young western larch trees, causing stem deformities and reduced height growth.

Western spruce budworm generally does not cause much injury in even-aged stands 1 to 20 years old. In an extensive study that included the range of budworm in Montana, defoliation of host trees seldom exceeded 25 percent even though adjacent, mature stands were often heavily defoliated (see footnote 11). At times, however, young western larch are seriously damaged because budworm larvae actually sever the terminal shoots (Figure 3) (Fellin and Schmidt 1973b; Schmidt and Fellin 1973). Strong apical dominance is characteristic of larch, and height growth soon returns to normal, most rapidly in the less dense stands (Schmidt 1978).

Understory trees or saplings in cutover areas near the borders of uncut, infested stands are more vulnerable to budworm than small trees in harvested stands. Ferguson and Stage[19] found significant height-growth reductions in defoliated understory trees, and growth losses increased with increasing defoliation. Much of the data, however, were taken from suppressed and intermediate shade-tolerant advance regeneration in stands harvested through the selection method; many of the trees were shade-tolerant species.

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[18] Arno, S.F. 1983. Personal communication during development of cooperative studies on effects of fire. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Northern For. Fire Lab., Missoula, MT.

[19] Ferguson, D.E.; Stage, A.R. 1982. Impact of defoliation by spruce budworm on growth and development of young timber stands in Idaho. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Moscow, ID. Rep. to CANUSA Spruce Budworms Program-West. 22 p.

Because seedling and sapling stands have low susceptibility to budworm, treatments specifically designed against budworm probably are not warranted. Nevertheless, thinning and regulation of species composition can only reduce the already low susceptibility in these young stands.

Pole Stands
Pole-size stands can be highly susceptible to western spruce budworm. In western Montana and presumably elsewhere in the western United States, thousands of acres now support these second-growth stands, many of which are overstocked and composed of shade-tolerant species that are ideal hosts (Arno 1976).

Commercial and precommercial thinning can reduce susceptibility in these problem stands. Radial-growth rate of residual shade-tolerant hosts doubled and defoliation was reduced from 60 percent before thinning down to 35 percent after treatment in a stand thinned to a spacing of 4.3 × 4.3 m (14 × 14 ft) (see footnote 12). Larval-dispersal loss likely increased and adult flight behavior was probably affected adversely — resulting in reduced oviposition on host trees. Vigor of trees likely increased and defensive chemistry was strengthened as the crowns responded to increased moisture and light. Further evidence for the benefits of thinning is presented by Schmidt and Fellin (1973). In western larch stands 20 to 30 years old, a higher percentage of trees were damaged at low stand densities when budworm populations were low, but no difference was found at high populations. When budworm populations subsided, however, trees in the thinned stands recovered much faster than in the unthinned.

Thinning, cleaning, and weeding can be done in intermediate-aged stands to alter stand factors affecting susceptibility — species composition, density, height-class structure, and vigor. Treatments increasing the proportion of seral hosts and nonhosts, increasing stand vigor, and encouraging the least diversity in height-class structure are most likely to create conditions least suitable for budworm.

Fertilizers — usually in one of several combinations of nitrogen, phosphorus, and potassium, (NPK) — have been applied to some western forests, particularly in the Pacific Northwest states, primarily to increase tree growth and vigor. Little research has been done, however, to determine if the application of one or more of those mineral nutrients affects host vulnerability. Schmidt and Fellin (1983) studied the effects of six combinations of NPK on the incidence of damage to young larch by the western spruce budworm. Some treatments showed little or no effect, but trees treated with nitrogen had consistently more larval damage to fascicle needles and severance of terminal and upper lateral shoots than untreated trees.

Effectiveness of the Silvicultural Approach

The silvicultural approach to dealing with western spruce budworm theoretically could reduce budworm to a less significant pest of western forests. Reducing the numbers and percent composition of its primary hosts and manipulating habitat for maximum larval mortality during dispersal, minimal egg-laying sites, modified adult behavior, and enhanced habitat for predators and parasites over the entire budworm range would effectively reduce forest susceptibility. Total habitat manipulation is impossible, however. Congressionally defined Wilderness areas, inaccessible roadless areas, and sites marginal for timber production will elude silvicultural treatments and, in all probability, will continue to be infested by budworm. Prevention of fire in Wilderness has led to the development of several millions of acres of good budworm habitat (Carlson et al., in press a). About the only tool available for reducing budworm habitat in Wilderness, backcountry, and marginal timber sites is prescribed fire; the philosophical basis for the use of prescribed fire in Wilderness is currently under debate, but recent decisions to allow natural fires to burn unchecked under certain conditions should reduce budworm habitat.

Within lands in the timber base — private, state, provincial, and federal — the silvicultural approach can be effective. We realize current infestations cannot be immediately curbed through silviculture; it will be a long-term process. But for individual stands, the treatment is immediately effective. A clearcut reduces budworm habitat 100 percent; other regeneration cuts reduce habitat proportionately less. Thinning to change species composition, increase vigor, or change the height-class structure is immediately effective stand by stand — susceptibility and vulnerability are reduced and, to some degree, the stand is protected against budworm. Furthermore, the protection is long term, unlike insecticide treatments.

Treatment effectiveness is more subtle over an entire forest. Consider a major forested drainage in which most of the stands are susceptible to budworm. Even-aged harvest methods or intermediate treatments in a few of the stands will have little effect on forest susceptibility. Through time, when most of the stands have received effective silvicultural treatment, the forest as a whole may be deemed relatively nonsusceptible. Whether or not susceptibility will be reduced forestwide will depend on forest economics, the political climate, and the dedication and perseverance of forest managers to the cause of intelligent forest management.

Silviculture and the Combined Prognosis-Budworm Simulation Model

The effectiveness of long-term management of forests to reduce hazard to budworm will depend on our ability to predict susceptibility as stands age. For an even-aged stand established after a clearcut, how long until the stand is at risk to budworm? Western silviculturists currently use the Prognosis Model, which simulates stand development (Stage 1973). This model uses tree records representing data from real stands and predicts tree and stand growth through time. The model has been revised several times; recently a submodel was added that predicts probability of stocking after harvest (Ferguson and Crookston 1984). A submodel simulating population dynamics of the western spruce budworm — the Budworm Model — will soon be linked to Prognosis, so that the interaction of the insect and the forest can be simulated — not only within a stand, but also between stands (Crookston 1985).

The combined model is not yet functional, but when it is, users should be able to predict when a stand will become susceptible to budworm, growth loss from expected defoliation, and budworm populations relative to stand characteristics and recent climate. The user will be able to simulate results of intermediate treatments on budworm populations. If the Combined Prognosis-Budworm Model performs as scientists hope, it could be the best tool for rating stand susceptibility and vulnerability.

Research Needs

Knowledge of the interactions between the western spruce budworm and its environment has increased substantially since the Canada-United States Spruce Budworms Program was initiated. For each question answered, however, many more have been raised. Our current understanding of how the budworm interacts with its environment is still incomplete. We believe that future research on the western spruce budworm should focus on the following unanswered questions:

- How far and how much do adults and larvae disperse? How is dispersal influenced by topography and stand conditions?
- What is the specific distribution of budworm by habitat type? What is its precise ecological amplitude?
- How do budworm populations differ genetically between geographic locations in western North America?
- Why are shade-tolerant conifers more susceptible and vulnerable to budworm than shade-intolerant hosts?
- Why do budworm feed differently on western larch than on other conifers?
- Does susceptibility of western larch decrease with tree age? If so, why?
- Are reproductive buds better substrate for budworm than foliage? Why? What factors regulate susceptibility and vulnerability of seeds and cones?
- How do forest fertilizers affect budworm dynamics?
- How does plant nutrient stress affect budworm dynamics? What is the biochemical basis of the relation between tree vigor and budworm development?
- How does intensive silviculture influence larval development, adult and larval dispersal, fecundity, and defoliation by budworm in immature forests?
- Were budworm populations and damage limited by forest fires before the early 1900s?
- How accurate are the present models used to estimate stand susceptibility and vulnerability to budworm? Which models are best?
- What factors cause budworm populations to remain sparse? How do these factors interact? Can the factors be modeled mathematically?

Answers to these questions would help us to develop management practices detrimental to the western spruce budworm.

Summary and Conclusions

The degree of susceptibility of forest stands to the western spruce budworm depends on several site and stand factors, such as composition, height-class structure, density, vigor, maturity of stands, and continuity of host type. Susceptibility is also strongly influenced by regional and site climate, which affect both the forest and the budworm. Climate affects budworm directly and indirectly through its effects on the forest. Western budworm outbreaks occur less frequently in cool, moist climates than in warm, dry ones.

The most susceptible forests are shade-tolerant conifers growing in multistoried, dense stands. These stands minimize mortality of dispersing larvae, provide ample sites for egg-laying, are usually stressed so that defensive chemistry is low, and provide maximum foliar biomass to feeding larvae.

Since the early to mid-1900s, two resource-management practices have substantially contributed to the increased susceptibility of vast acreages of forests in the western United States. One factor has been an aggressive program for preventing and controlling fire, which has substantially reduced fire frequency and the acreage of forests burned. The second factor is the all-aged or uneven-aged management practiced extensively during the early to mid-1900s. Both of these practices have contributed to the development of highly susceptible forests by creating multistoried stands, usually densely stocked and often made up largely of shade-tolerant conifers that are host for budworm.

Considerable progress has recently been made in understanding the relation between budworm population dynamics and coniferous forest-stand dynamics. The combined Prognosis-Budworm Model is nearly developed and should be useful for simulating interactions of budworm and stands. We have also developed methods for rating susceptibility of stands and ranking them for silvicultural treatment.

Silvicultural practices can be used to minimize stand susceptibility. These treatments can have both immediate and long-term effects stand by stand. Minimizing the susceptibility of conifer forests is a longer term objective, however, and depends on the intensity of treatments prescribed. Even-aged silvicultural practices encouraging the establishment and growth of seral species are most effective in reducing forest susceptibility. Uneven-aged practices may also be effective under certain conditions. Intermediate treatments, such as thinning and cleaning, in immature stands also help to minimize susceptibility. Salvage or presalvage may have limited value in mature stands.

Based on our research and on current understanding of the complex interrelations of the forest and the western spruce budworm, we believe the following silvicultural practices can be used to create more vigorous forests, while creating a habitat and environment less favorable for the western spruce budworm:

- Strive for stand diversity in species composition by favoring seral trees and removing or otherwise discriminating against the most shade-tolerant host trees.
- Regulate stand density through appropriate release cuttings and thinnings to improve and maintain tree vigor and stand growth.
- Create and maintain even-aged stand structures by using even-aged regeneration systems, followed by periodic low and crown thinnings.
- Promptly remove all overwood trees once regeneration is established in seed-tree and shelterwood cuttings.
- Improve stand vigor by removing diseased, heavily infested, or otherwise unhealthy trees in all cuttings.
- Capitalize on phenotypic and genetic resistance to budworm by selecting the most heavily defoliated trees for removal. Retain the lightly or nondefoliated trees for seed trees; direct cone-collection programs to those phenotypes.
- Regenerate host stands at or before biological maturity as indicated by the culmination of annual growth.
- Diversify the host forest by creating seral stands in homogeneous areas of late successional or climax stands.

Literature Cited

Arno, S.F. 1976. The historical role of fire on the Bitterroot National Forest. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-187. 29 p.

Arno, S.F. 1979. Forest regions of Montana. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-218. 39 p.

Arno, S.F. 1980. Forest fire history in the northern Rockies. J. For. 78(8):460-465.

Beckwith, R.C.; Burnell, D.G. 1982. Spring larval dispersal of the western spruce budworm (Lepidoptera: Tortricidae) in north-central Washington. Environ. Entomol. 11(4):828-832.

Blais, J.R. 1958. The vulnerability of balsam fir to spruce budworm attack in northern Ontario, with special reference to physiological age of the tree. For. Chron. 34(4):405-422.

Campbell, R.W. (In press). Population dynamics. Chapter 6 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech. coords. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1694.

Campbell, R.W.; Carlson, C.E.; Theroux, L.J.; Egan, T.H. 1984. Some effects of predaceous birds and ants on the western spruce budworm on conifer seedlings. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-315. 5 p.

Carlson, C.E.; Fellin, D.G.; Schmidt, W.C. 1983. The western spruce budworm in northern Rocky Mountain forests: a review of ecology, insecticidal treatments and silvicultural practices. Pages 76-103 *in* J. O'Loughlin and R.D. Pfister, eds. Management of second-growth forests: the state of knowledge and research needs. Proc. Symp., Mont. For. and Conserv. Exp. Stn., Univ. Mont., Missoula, MT.

Carlson, C.E.; Schmidt, W.C.; Fellin, D.G. (In press). a. The role of fire in western spruce budworm dynamics: is wilderness a factor? Proc., Wilderness Fire Symp., Missoula, Mont. U.S. Dep. Agric., For. Serv., Ogden, UT. Gen. Tech. Rep.

Carlson, C.E.; Schmidt, W.C.; Wulf, N.W. (In press). b. Silvicultural treatment. *In* Chapter 7, M.H. Brookes, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech. coords. Managing trees and stands susceptible to western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1695.

Carlson, C.E.; Theroux, L.J. 1982. Predicting intensity of western spruce budworm radial growth reduction in western Montana forests. Northwest Sci. Assoc. 55th Annu. Meet., Walla Walla Coll., Walla Walla, Wash. Abstract.

Carolin, V.M.; Coulter, W.K. 1975. Comparison of western spruce budworm populations and damage on grand fir and Douglas-fir trees. U.S. Dep. Agric. For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-195. 16 p.

Cates, R.G.; Redak, R.A.; Henderson, C.B. 1983. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions. Pages 3-19 *in* P.A. Hedin, ed. Plant resistance to insects. Symp., Am. Chem. Soc., Washington, D.C. No. 208.

Chrisman, A.B.; Black, G.M.; Shearer, R.C. 1983. Effect of western spruce budworm on Douglas-fir cone production in western Montana. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-308. 7 p.

Crookston, N.L. 1985. Forecasting growth and yield of budworm-infested forests: Part II: Western North America and summary. Pages 214-230 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Daubenmire, R.; Daubenmire, J. 1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agric. Exp. Stn., Wash. State Univ., Pullman, Wash. Tech. Bull. 60. 104 p.

DeByle, N.V.; Packer, P.E. 1981. Soils and watershed. Pages 47-52 *in* N.V. DeByle, ed. Clearcutting and fire in the larch-Douglas-fir forests of western Montana — a multifaceted research summary. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-99.

Despain, D.W. 1981. Vegetation, site, and distribution characteristics of spruce budworm infested Douglas-fir communities in southwestern Montana. Wash. State Univ., Pullman, Wash. M.S. Thesis, 103 p.

Dickman, A. 1978. Reduced fire frequency changes species composition of a ponderosa pine stand. J. For. 76:24-25.

Fauss, D.L.; Pierce, W.R. 1969. Stand conditions and spruce budworm damage in a western Montana forest. J. For. 67(5):322-325.

Fellin, D.G. 1980. The western spruce budworm in the American Rocky Mountains. CANUSA Newsl. (Int. Spruce Budworms Program, Ottawa, Ont.) 8:1-3.

Fellin, D.G. 1983. Chemical insecticides vs. the western spruce budworm: after three decades, what's the score? Western Wildlands (Univ. Mont., Missoula, Mont.) 9(1):8-12.

Fellin, D.G.; Dewey, J.E. 1982. Western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. For. Insect and Dis. Leafl. 53. 10 p.

Fellin, D.G.; Schmidt, W.C. 1967. Spruce budworm larvae sever stems of western larch shoots in Montana. J. For. 65(4):258-260.

Fellin, D.G.; Schmidt, W.C. 1973a. Frost reduces western spruce budworm populations and damage in Montana. Agric. Meteorol. 11:277-283.

Fellin, D.G.; Schmidt, W.C. 1973b. How does western spruce budworm feeding affect western larch? U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-7. 35 p.

Fellin, D.G.; Shearer, R.C.; Carlson, C.E. 1983. Western spruce budworm in the northern Rocky Mountains: biology, ecology, and impacts. Western Wildlands (Univ. Mont., Missoula, Mont.) 9(1):2-7.

Ferguson, D.E.; Crookston, N.L. 1984. User's guide to the Regeneration Establishment Model — a Prognosis Model extension. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-161. 23 p.

Garrison, G.A.; Bjugstad, A.J.; Duncan, D.A.; Lewis, M.E.; Smith, D.R. 1977. Vegetation and environmental features of forest and range ecosystems. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. WO-475. 68 p.

Greenbank, D.O. 1963. Staminate flowers and the spruce budworm. Pages 202-218 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. No. 31.

Gruell, G.; Schmidt, W.C.; Arno, S.F.; Reich, W. 1982. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana — implications for resource management. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-130. 42 p.

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of the western spruce budworm in the American northern Rocky Mountain area from 1922 through 1971. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-20. 144 p.

McDonald, G.I. 1979. Resistance of Douglas-fir to western spruce budworm: results of a preliminary progeny test. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Note INT-264. 7 p.

McDonald, G.I. 1981. Differential defoliation of neighboring Douglas-fir trees by western spruce budworm. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Note INT-306. 10 p.

McDonald, G.I. (In press). Heritability of resistance in Douglas-fir to western spruce budworm. Proc. IUFRO Workshop: Role of host-pest interaction in the dynamics of forest insects. Banff, Alberta. 4-7 September 1983.

Mott, D.G. 1963. The forest and spruce budworm. Pages 189-202 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. No. 31.

Pfister, R. 1981. Habitat type classifications for managing western watersheds. Pages 59-67 *in* D.M. Baumgartner, ed. Interior west watershed management. Proc. Symp. Wash. State Univ., Pullman, Wash.

Pfister, R.D.; Kovalchik, B.L.; Arno, S.F.; Presby, R.C. 1977. Forest habitat types of Montana. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-34. 174 p.

Schmidt, W.C. 1978. Some biological and physical responses to forest stand density. *In* Proc. Eighth World For. Congr., 16-20 October 1978. P.T. Gramedia, Jakarta, Indonesia. 12 p.

Schmidt, W.C.; Fellin, D.G. 1973. Western spruce budworm damage affects form and height growth of western larch. Can. J. For. Res. 3(1):17-26.

Schmidt, W.C.; Fellin, D.G. 1983. Effect of fertilization on western spruce budworm feeding in young western larch stands. Pages 87-96 *in* Proc., Forest defoliation-host interactions: a comparison between gypsy moth and spruce budworms. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Stn., Broomall, Pa. Gen. Tech. Rep. NE-85.

Schmidt, W.C.; Fellin, D.G.; Carlson, C.E. 1983. Alternatives to chemical insecticides in budworm-susceptible forests. Western Wildlands (Univ. Mont., Missoula, Mont.) 9(1):13-19.

Shepherd, R.F. 1959. Phytosociological and environmental characteristics of outbreak and non-outbreak areas of the two-year cycle spruce budworm, *Choristoneura fumiferana*. Ecology 40(4):608-620.

Smith, D.M. 1962. The practice of silviculture. 7th ed. John Wiley & Sons, New York. 578 p.

Society of American Foresters. 1971. Terminology of forest science, technology practice and products. F.C. Ford-Robinson, ed. Soc. Am. For., Washington, D.C. 349 p.

Stage, A. 1973. Prognosis model for stand development. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-137. 32 p.

Stark, N.M. 1979. Nutrient losses from timber harvesting in a larch/Douglas-fir forest. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Res. Pap. INT-231. 41 p.

Steele, R.; Cooper, S.V.; Ondov, D.M.; Roberts, D.W.; Pfister, R.D. 1983. Forest habitat types of eastern Idaho-western Wyoming. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-144. 122 p.

Steele, R.; Pfister, R.D.; Ryker, R.A.; Kittams, J.A. 1981. Forest habitat types of central Idaho. U.S. Dep. Agric., For. Serv., Intermt. For. and Range Exp. Stn., Ogden, UT. Gen. Tech. Rep. INT-114. 138 p.

Sutherland, M.G. 1983. Relationship of site and stand characteristics to outbreaks by western spruce budworm in the Bitterroot National Forest. Wash. State Univ., Pullman, Wash. M.S. Thesis. 54 p.

Twardus. D.B. 1980. Evaluation of weather patterns in relation to western spruce budworm outbreaks in north-central Washington, 1970-1980. U.S. Dep. Agric., For. Serv., Pac. Northwest Region, Portland, OR. Misc. Rep. 16 p.

Ulrich, B. 1983. A concept of forest ecosystem stability and of acid deposition as driving force for destabilization. Pages 1-29 *in* B. Ulrich and J. Pankrath, eds. Effects of accumulation of air pollutants in forest ecosystems. D. Reidel Publ. Co., Boston.

Wagg, J.W.B. 1958. Environmental factors affecting spruce budworm growth. For. Lands Res. Cent., Corvallis, OR. Res. Bull. 11. 27 p.

Wellington, W.G. 1949. The effects of temperature and moisture upon the behavior of the spruce budworm. II. The responses of larvae to gradients of evaporation. Sci. in Agric. 29:216-229.

Willhite, E.A.; Stock, M.W. 1983. Genetic variation among western spruce budworm *Choristoneura occidentalis* (Lepidoptera: Tortricidae) outbreaks in Idaho and Montana. Can. Entomol. 115:41-54.

Williams, C.B., Jr. 1966. Differential effects of the 1944-56 spruce budworm outbreak in eastern Oregon. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-33. 16 p.

Williams, C.B., Jr. 1967. Spruce budworm damage symptoms related to radial growth of grand fir, Douglas-fir, and Engelmann spruce. For. Sci. 13(3):274-285.

Williams, C.B., Jr.; Shea, P.J.; Walton, G.S. 1971. Population density of western spruce budworm as related to stand characteristics in the Bitterroot National Forest. U.S. Dep. Agric., For. Serv., Pac. Southwest For. and Range Exp. Stn., Berkeley, CA. Res. Pap. PSW-72. 8 p.

Wulf, N.W.; Carlson, C.E. (In press). Rating stand hazard to western spruce budworm. *In* Chapter 6, M.H. Brookes, R.W. Stark, R.G. Mitchell, and J.J. Colbert, eds. Managing trees and stands susceptible to western spruce budworm. U.S. Dep. Agric., Washington, D.C. Tech. Bull. 1695.

Wulf, N.W.; Cates, R.G. (In press). Site and stand characteristics related to budworm density and tree damage. Chapter 7 *in* M.H. Brookes, R.W. Campbell, R.W. Stark, R.G. Mitchell, and J.J. Colbert, eds. Western spruce budworm. U.S. Dep. Agric., Washington, D.C. Tech. Bull. 1694.

Tactics and Strategies for Larval Suppression and Prevention of Damage using Chemical Insecticides

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Management of the spruce budworms in North America over limited areas has been achieved through the aerial application of insecticides. Aerial sprays were first applied in 1949; although significant advances have been made in the development of insecticides that are more effective and more environmentally acceptable than DDT (e.g. fenitrothion, aminocarb) certain aspects of aerial spraying still need to be improved. Research has shown that the optimum droplet size for budworm control is between 30 and 50 microns; however, spray atomization equipment is not available to the operator to consistently produce a spray cloud with these drop size characteristics. The guidance of spray aircraft over a forested area is a problem that appears to be close to resolution. Large multi-engined spray aircraft use an inertial guidance system. Smaller, relatively less expensive guidance systems are being field tested and although they show potential for use and are being used operationally under certain conditions, they are still too expensive for many operations. Modeling of spray cloud behavior indicates that presently accepted and used guidelines for suitable weather for spray application are incorrect. Field trials to test the models are being planned. If the models prove to be correct the whole concept of aerial spraying will change with a resultant improvement in efficacy. After 35 years of operational spraying the tactics and strategies used remain basically unchanged with sprays still being aimed at the later instars and the objective of the spray being foliage protection.

En Amérique du Nord, la lutte antitordeuse sur des superficies forestières limitées a été menée au moyen d'épandages aériens d'insecticides. Ces premiers épandages datent de 1949, et malgré la mise au point d'insecticides tels que le fénitrothion et l'aminocarbe qui sont plus efficaces et plus écologiques que le DDT, certains aspects restent à améliorer. Les recherches ont démontré que la taille optimale des gouttelettes se situe entre 30 et 50 microns; cependant, le matériel capable de pulvériser des gouttelettes de cette taille reste inaccessible aux épandeurs. Le guidage des avions pose des difficultés qui sont près d'être résolues. Le système utilisé par les gros multimoteurs est inertiel, tandis que des systèmes plus petits et relativement moins coûteux sont expérimentés sur le terrain. Même si ces derniers sont prometteurs et sont déjà utilisés dans certaines conditions, ils sont encore souvent trop coûteux. La modélisation du comportement du nuage pulvérisé montre que les critères météorologiques actuels sur lesquels on se fonde pour les épandages sont inexacts. On prévoit des essais sur le terrain pour vérifier ces modèles. Si ceux-ci sont confirmés, la stratégie des pulvérisations aériennes sera transformée, au profit d'une amélioration de l'efficacité. Après 35 ans de campagnes, les tactiques et les stratégies ont fondamentalement peu changé, les traitements étant surtout appliqués aux derniers stades larvaires, avec comme objectif la protection du feuillage.

Introduction

Historically the spruce budworms of North America, *Choristoneura fumiferana* (Clem.), and *Choristoneura occidentalis* Free., have played a role in the development of our forests as we know them today. Periodic outbreaks of these insects have killed balsam fir (*Abies balsamea* (L.) Mill), spruce (*Picea* spp.), Douglas-fir (*Pseudotsuga menziesii* (Mirb) Franco), Engelmann spruce (*Picea engelmannii* Parry) and grand fir (*Abies grandis* (Dougl.) Lindl.) over extensive areas. In eastern North America in particular, the outbreaks of spruce budworm have occurred fairly regularly at 30-50 year intervals. Blais (1981) reviewed the sequence of epidemics; from ring-growth studies he was able to identify epidemics back into the early 18th century. In western North America the first report of an outbreak of the western spruce budworm was in 1922 (Johnson and Denton 1975).

North America was once thought by many to be a land of limitless forests, and harvesting practices were such that man and the budworms could co-exist. Even under conditions of a budworm epidemic there was no shortage of available wood. Even if forest managers had wanted to apply a chemical to control the spruce budworm, there was no effective way to do so until aircraft were developed that could carry a load greater than the pilot and fuel. Johansen (1913) first suggested the use of aircraft for chemical application. The first test in the United States was carried out in 1921 (Balch et al. 1955/56). For this first aerial protection program, a Curtis J.N.6 aircraft was used to apply lead arsenate dust. The first Canadian aerial application was in Nova Scotia in 1927, followed by treatments in Ontario in 1928 and 1929 (Prebble 1975). The insecticide used in Canada was a calcium arsenate dust.

In subsequent years aircraft were used to apply insecticides to forested areas in Germany, Czechoslovakia, Poland, France, Russia, South Africa, and Australia. Balch et al. (1955/56) give an excellent summary review of these early programs. These treatments were all with dusts and met with only limited success. The major problems encountered were the relatively large amounts required to provide protection (more than 10kg/ha [9 lb/acre] [Prebble 1975]) and the physical properties of the dust. Weather was critical in a dust application; unless it was calm with no thermal updrafts the dust did not settle. Rainfall shortly after a dust application was also a problem in that it washed the dust off the foliage. Even in the early days there was an acknowledged need for an effective guidance system to ensure that the aircraft would provide uniform coverage to extensive forested areas that could not be marked using the techniques available to agricultural aerial application (flag men, markers, or easily recognizable features in the treatment area).

The breakthrough in insect control came during and just after the Second World War. Although the insecticide DDT was discovered in 1939, its full potential was not realized until wartime conditions required the treatment of large areas for malaria mosquito control and the treatment of large numbers of people for body louse control (Brown 1951). DDT appeared to be the panacea; it was very effective as an insecticide at the rates used, it was safe to humans, and it could be mixed to give a dust, wettable powder, oil suspension, emulsion or oil solution. The amounts required were, by the standards of those days, minimal (1 kg/ha, 0.9 lb/acre), and it was cheap. Added to this was DDT's long residual life and if it did not kill the insect by direct contact, the residual deposit killed any insect that came in contact either by ingestion or walking across the treated area. DDT usage increased dramatically around the world with rapid developments in application technology being made by researchers and operators in both the United States and Canadian Forest Services.

Other factors that played significant roles in the development of effective forest aerial spray programs were the availability of aircraft and pilots. With the cessation of war activities, large numbers of well-trained pilots as well as surplus military aircraft were available. The Stearman aircraft, built by Boeing was a rugged airplane capable of carrying a payload of about 400 kg (880 lb). Replacement of the front cockpit with an insecticide tank converted it to an ideal spray plane. The Stearman was the backbone of the early post-war budworm spray programs.

Early Operational Programs

Outbreaks of the western spruce budworm in Oregon and Washington in 1945 and of the eastern spruce budworm at about the same time in Ontario and Quebec resulted in decisions to attempt to control the insect populations using DDT applied by air (Balch et al. 1955/56). The first large-scale operations were in Oregon and Washington, in which 108 000 ha (270,000 acres) were treated in 1949 (Balch et al. 1955/56). In New Brunswick and Quebec, 113 360 ha (280,000 acres) were treated in 1952 (Prebble 1975). DDT was applied as an oil solution at the rate of 1.2 kg/ha (1 lb/acre) in 9.35 L/ha (1 gal/acre). These spray programs were considered successes. As examples of the expanded use of DDT, almost 400 000 ha (1.0 million acres) were treated in Oregon and Washington in 1951 (Balch et al. 1955/56); 804 400 ha (1.9 million acres) were treated in New Brunswick and Quebec in 1953 (Prebble 1975): and in Montana, Idaho and Wyoming, 144 000 ha (350,000 acres) were treated in 1955 (Fellin 1983). The pattern of increasing DDT usage continued until first reports of fish kill (Prebble 1975) were recorded in Canada.

Outbreaks of spruce spider mite were reported on 200 000 ha (0.5 million acres) of treated forest in Washington, Montana, Idaho and Wyoming (Fellin 1983), and forest managers noted generally that budworm were reinfesting sprayed areas. Concern over the impact of DDT on the forest ecosystem had been acknowledged with its first use. Brown (1951) made the following interesting comment about chemical insecticides and the need to use them to protect our health, agriculture, and forest resources from insect attack:

> "To this end the economic entomologist must develop selective poisons for particular arthropod species; or rather, since this is not biochemically likely, he must apply them in such a way and at such a dosage level that they become selective to hit the target species alone."

Insecticide Development

The concern over the impact of DDT on the environment, plus a desire to improve the efficiency of spray programs, stimulated researchers to identify new insecticides that were more selective and could be applied at lower dosage rates, and new techniques to improve spray application. Flieger (1953) showed that DDT applied at 0.5 kg/ha (0.5 lb/acre) could be just as effective as DDT applied at 1.12 kg/ha (1 lb/acre) if care was taken to have the aircraft suitably calibrated. In the western United States, malathion was tested in 1963; shortly thereafter phosphamidon and naled were tested (Fellin 1983). In the State of Maine, malathion was tested at 0.5 kg (0.5 lb/acre) in 1964 (Morrison and Dimond 1978). Extensive continuous screening programs of newly available chemicals were carried out at a USDA Forest Service laboratory of the Insecticide Evaluation Project at Berkeley, California; in Canada, the Canadian Forestry Service, Forest Pest Management Institute at Sault Ste. Marie, Ontario, continued the screening begun by the Chemical Control Research Institute in Ottawa.

These screening programs identified new, promising chemicals for spruce budworms control. Over the years, literally hundreds of chemicals developed primarily for the agricultural market, were evaluated. The test protocols used by both the American and Canadian researchers were basically similar: laboratory studies to determine toxicity to selected instars of the spruce budworms, studies to determine longevity of the deposit on foliage under weathering conditions, individual tree treatments, small-scale field trials (using aircraft), semi-operational or demonstration trials and finally, following registration of the product, operational use. The common, scientific, and registered trade names of the products that were field tested or applied operationally for control of spruce budworms in North America are listed in Table 1. Some compounds which were used only once on a very small area, i.e., 10 ha (25 acres), or which were found ineffective have not been included in the list. Field trials were carried out with mexacarbate in the Nezperce National Forest (Dewey et al. 1971), in the northern Rocky Mountains in 1965 (Fellin 1983), the State of Maine in 1967 (Morrison and Dimond 1978). In 1976 trichlorfon and acephate were tested in Montana (Flavell et al. 1977). In Canada BHC was tested in 1953, dimethoate in 1962, fenitrothion and aminocarb in 1965, to name but a few (Prebble 1975). The insecticides that were used operationally on spruce budworms programs in North America are shown in Table 2.

The total number of chemical insecticides used in each country is nine, the only difference being the use of phosphamidon in Canada and malathion in the United States to replace DDT. The principal use of mexacarbate was in the United States where it was applied on operational programs in both the eastern and western states. Mexacarbate was only used operationally or for very large trials in Canada from the late 1960s to 1973. The insecticide carbaryl had only limited use in Canada, in New Brunswick in 1958, and in Manitoba in 1973 (Nigam 1975), but was extensively used in the United States where it was the principal insecticide for the period 1975 to 1982 (D. Kucera, personal communication 1984).

In this review the insecticide *Bacillus thuringiensis* (B.t.) must not be forgotten. Forest managers were aware of the problems associated with chemical insecticides, and although B.t. had been identified and tested in 1960 against the blackheaded budworm (*Acleris gloverana* (Wals.)) on the Queen Charlotte Islands in British Columbia (Lejeune 1975), in New Brunswick the same year (Morris et al. 1975), and in the State of Maine in 1963 (D. Kucera, personal communication 1984), the use of B.t. had never met with universal approval. Cunningham (1985), in his review of biorationals for control of the spruce budworms, has outlined the history of the development of B.t. to its successful, large-scale use in 1984 when over 400 000 ha (1.0 million acres) were treated in Canada.

Spray Application Technology and Deposit Assessment

Concurrent with the development of new insecticides was work on spray application equipment and tests of different types of aircraft. Studies on guidance systems were also carried out to ensure that the aircraft flew a proper flight pattern to prevent misses or double swathing. The standard spray equipment used was the boom and nozzle system developed for agricultural work. In Canada, as early as 1953, the standard DDT tank mix, properly atomized, was found to provide

Table 1

Common, scientific, and trade names of chemical insecticides field tested experimentally and operationally against spruce budworms[1,2]

1.	acephate	*O, S* - dimethyl acetylphos-phoramidothioate	Orthene®
2.	aminocarb	4 - dimethylamino-m-tolyl methylcarbamate	Matacil®
3.	azamethiphos	5-6-chloro-2-oxo-oxazolo [4-5-b] pyridin-3-ylmethyl 0.0-dimethyl phosphorothioate	Alfacron®
4.	benzene hexachloride	1, 2, 3, 4, 5, 6 - hexachlorocyclohexane, mixed isomers and a specified percentage of gamma	gammexane, BHC
5.	carbaryl	1-naphthyl methylcarbamate	Sevin®
6.	chlorpyrifos-methyl	0,0 - dimethyl 0-(3, 5, 6 - trichloro-2-pyridyl) phosphorothioate	Reldan®
7.	DDT	1, 1, 1 - trichloro - 2, 2-bis-(*p*-chlorophenyl) ethane	DDT
8.	dichlorvos	2, 2 - dichlorovinyl dimethyl phosphate	Vapona®
9.	dieldrin	not less than 85% of 1, 2, 3, 4, 10, 10 - hexachloro - 6, 7- epoxy - 1, 4, 4a, 5, 6, 7, 8a octahydro - 1, 4 - endo-exo - 5, 8 - dimethanonaphthalene	Octalox®
10.	dimethoate	0,0 - dimethyl S - (N-methylcarbamoylmethyl) phosphorodithioate	Cygon®
11.	diflubenzuron	1-(4-chlorophenyl) -3-2 (2,6-diflurobenzoyl) urea	Dimilin®, TH60-40
12.	fenitrothion	*0,0* - dimethyl *0* - (4 nitro-m-tolyl) phosphorothioate	Sumithion®, Accothion®, Novathion®, Folithion®
13.	fenthion	*0,0* - dimethyl 0 -[4-(methylthio)-m-tolyl] phosphorothioate	Baytex®, Entex®
14.	iodofenphos	0 (2,5-dichloro-4-iodophenyl) 0,0-dimethyl phosphorothioate	Nuvanol®
15.	malathion	diethyl mercaptosuccinate. S-ester with 0,0- dimethyl phosphorodithioate	Malathion, Cythion®
16.	methomyl	methyl N-[(methylcarbamoyl)oxy] thioacetimidate	Lannate®, Nudrin®
17.	mexacarbate	4-dimethylamino-3,5 xylyl methylcarbamate	Zectran®
18.	naled	1,2-dibromo-2,2-dichloroethyl dimethyl phosphate	Dibrom®
19.	permethrin	3 phenoxybenzyl (+)Trans-3-(2,2-dicalorovinyl)-2,2-dimethyl-cyclopropanecarboxylate	Ambush®
20.	phosmet	0,0-dimethyl S-phthalamidomethyl phosphorodithioate	Imidan®
21.	phosphamidon	2-chloro-*N,N*-diethyl-3 hydroxycrotonamide dimethyl phosphate	Dimecron®
22.	phoxim	phenylglyoxylonitrile oxime 0,0-diethyl phosphorothioate	Volaton®
23.	propoxur	0-isopropoxyphenyl methylcarbamate	Baygon®, Unden®
24.	pythrethrins	pyrethrum (principally from plant species (*Chrysanthemum cinariaefolium*)	pyrethrin

Table 1 **(Concluded)**

25.	resmethrin	(5 benzyl-3 furyl) methyl 2,2-dimethyl-3-(2-methylpropenyl) cyclopropanecarboxylate	SBP 1382
26.	ronnel	0,0-dimethyl 0-2, 4, 5-trichlorophenyl phosphorothioate	Korlan®, Ronnel®
27.	stirofos	2-chloro-1-(2, 4, 5-trichlorophenyl) vinyl dimethyl phosphate	Gardona®
28.	TDE	1,1-dichloro-2,2-bis(p-chlorophenyl)ethane	Rhothane®
29.	temephos	0,0-dimethyl phosphorothioate 0,0-diester with 4,4′ thiodiphenol	Abate®
30.	toxaphene	chlorinated camphene containing 67-69% chlorine	Camphechlor®
31.	trichlorfon	dimethyl (2,2,2-trichloro-1-hydroxyethyl) phosphonate	Dylox®, Dipterex®

[1] Common, and scientific names from Kenaga and End (1974), Worthing (1979), and Common Names for Pest Control Chemicals (1982)

[2] Use of a registered Trade name does not imply endorsement of the product by either the Canadian Forestry Service or USDA Forest Service.

Table 2
Insecticides used operationally for control of spruce budworms in the United States and Canada

United States	Canada
DDT	DDT
Carbaryl	Carbaryl
Malathion	Phosphamidon
Mexacarbate	Mexacarbate
Fenitrothion	Fenitrothion
Aminocarb	Aminocarb
Acephate	Acephate
Trichlorfon	Trichlorfon
B.t.	B.t.

acceptable budworm control at 4.67 L/ha (0.5 gal/acre) (Flieger 1953). This reduction in volume resulted in a doubling of treatment area per sortie by the spray aircraft and hence a more economical program. Further volume reductions were achieved with fenitrothion (A.P. Randall and J.A. Armstrong, personal communication 1969), a 98 percent solution applied at 0.75 L/ha (0.08 gal/acre) using a Grumman Ag Cat fitted with Micronair® AU3000 units was shown to be effective and an average insect mortality of 90 percent was achieved. The reduction in the amount of active ingredient applied resulted in an effective treatment only when the spray was atomized to produce droplets in the appropriate size range. Himel (1969) showed that the most efficient drops were those "small enough to be produced in maximum numbers for maximum coverage and large enough to have optimum critical impingement velocity for optimum impingement on the target insect." Joyce (1975) coined the phrase "Biologically Optimum Droplet Size (BODS)" for the droplets of a specific size range to ensure maximum deposit, coverage, and insect kill. This critical relationship between droplet size, number of droplets deposited and percentage kill had been acknowledged earlier by Hurtig, Fettes and Davis (Fettes 1960). Akesson et al. (1969) showed that other factors to be considered in the search for the biologically optimum droplet size were the chemical and physical formulation used, and the type of crop.

In the early days of forest aerial spraying, efficiency in terms of coverage of the foliage was determined indirectly. Hurtig et al. (1953) showed that, for the coarse DDT sprays used, spray deposit recorded on a Kromekote® card at ground level in a clearing on the upwind side of a tree was similar to the deposit on the upper, outer, upwind portion of the tree crown. The use of Kromekote® cards became the standard device for spray deposit measurement in both the United States and Canada. In a Spray Deposit Assessment Workshop (1976) sponsored by the USDA Forest Service FIDM Methods Applications Group, the USDA Expanded Douglas-fir Tussock Moth Program, and the USDA Expanded Gypsy Moth Program, Kromekote® cards and sample plates were recommended as part of the deposit sampling technique. Even with this recommendation, it was acknowledged the ground sample units were not providing the desired information; the target was the conifer needle and that was the area that needed to be sampled. The use of artificial sampling surfaces was a matter of concern, even though they were economical, because many researchers used them for nothing more than to record the presence or absence of a deposit and the uniformity of treatment of the spray block. Himel (1969), in reference to the work by Potts (1958), Brooks (1947), and Latta et al. (1947), argued that there was a unique bias of large flat smooth objects (i.e., Kromekote® cards, aluminum plates) *against* the impaction of droplets smaller than 50 microns.

In an earlier study, Himel and Moore (1967) demonstrated that the highest mortality of western spruce budworm treated with mexacarbate occurred with droplets less than 50 microns in size. By direct measurement of droplets on needles, budworm larvae, and flat collecting surfaces, Barry et al. (1977) showed that the flat sample plates were biased to collecting larger droplets than were found on the larvae or needles, and that the collection efficiency was affected by the wind speed. Table 3 shows the percentage of particles found on each surface. Table 4 shows the relationship of impaction efficiency to wind speed.

Barry and Ekblad (1978) showed that 86 to 94 percent of the aerodynamic drops deposited on Douglas-fir and Engelmann spruce needles were equal to or less than 61 microns in diameter. In Canada, Randall (1975) demonstrated that effective control could only be achieved with a finely atomized spray and the aim of aircraft calibration projects was to produce a spray cloud with a Volume Median Diameter (VMD) of 80-90 microns, a Number Median Diameter (NMD) of about 60 microns and a Dmax (diameter of the largest drop) of about 150-200 microns.

Although there have been many questions asked about the efficiency and accuracy of Kromekote® cards, or similar flat collecting surfaces for representing the spray deposit on the tree, the technique is still used and recommended in guides for spray operators (Barry et al. 1978). Snowden et al. (1977) compared spray deposits on ground sample units with deposits on and within the tree crown; although deposits at ground level were reportedly less than in the upper crown, they were similar to leeward side cards and deposits on cards on the lower crown. Maksymiuk et al. (1975) reported that about twice as many droplets were collected on sample cards in forest openings as on cards placed under the canopy of the tree. Barry et al. (1980), in a direct measurement of droplets on needles, also reported the gradation in number of droplets deposited, with the largest number being on the upper crown. In a chemical analysis of spray deposits on white spruce trees, Armstrong and Yule (1978) showed that all parts of the tree received a deposit from the spray, there was more deposit on the upper crown than on the lower crown, and there was more deposit on the outer upwind portions of the tree than the inner and downwind portions. The use of Kromekote® sampling cards continued to be questioned. Spray operators

Table 3
Distribution by percentage of particles found on three collection surfaces, Lolo National Forest, Montana, 1972 [1]

Particle size		Collection surfaces		
Categories (µm)	Size distribution (%)[a]	Impaction plates	Western spruce budworm larvae	Douglas-fir needles
6	94.54	15.2	10.7	60.8
6-10	3.92	6.5	50.7	25.8
11-25	0.14	9.6	25.3	9.3
16-20	0.28	13.5	8.7	2.6
21-25	0.14	6.8	3.3	0.5
25	0.7	48.4	1.3	1.0

[a] Particle size distribution of the spray formulation

[1] Table from Barry et al. 1977

Table 4

Particle size associated with maximum impaction efficiency, as a function of wind speed, on Douglas-fir foliage, western spruce budworm, and glass slides (according to Sell's Theory), Lolo National Forest, Montana, 1972 [1]

Object (diam)	Wind speed (m/sec)	Particle size (μm)
Douglas-fir needle (1.59 mm)	0.447	35
	0.894	25
	1.341	20
	1.788	18
	2.682	14
	3.576	13
	4.470	11
Budworm (3.18 mm)	0.447	50
	0.894	35
	1.341	29
	1.788	25
	2.682	20
	3.576	18
	4.470	16
Plates (25.4 mm)	0.447	141
	0.894	100
	1.341	82
	1.788	71
	2.682	58
	3.576	50
	4.470	45

[1] Table from Barry et al. 1977

found themselves in the position of not being able to answer the questions of the public concerning where the spray was being deposited. This was especially crucial since reports such as that of Armstrong (1977) had indicated that, with Kromekote® cards as a sample surface, an average about 20-30 percent of the emitted spray reached the ground. If the hypothesis of Hurtig et al. (1953) was accepted, this suggested that a similar amount was impinging on the tree, and that up to 70-80 percent of the spray was not deposited in the target area. To provide answers to this crucial question and others about spray application in general, Forest Protection Limited in New Brunswick, Canada, undertook the responsibility of funding research through universities, the National Research Council of Canada, and the New Brunswick Research and Productivity Council to supplement the federal Canadian Forestry Service (CFS) program (Irving and Webb 1981).

Aircraft Guidance

The identification of spray blocks has long been a problem in forest aerial spray programs. The pilot of an agricultural spray aircraft treats a field of a specific crop that is recognizable and usually defined by fences, roads or significant boundaries. In the forest such boundaries do not exist; the pilot is forced to fly over seemingly endless forest and although it may be possible to locate the area with aerial photographs and maps, the pilot is then faced with flying a spray pattern with uniformly spaced swaths, and starting and finishing spray runs at set points to avoid contaminating nontarget areas. In attempts to provide guidance to the pilot, balloons have been used (Hurtig et al. 1953; J.A. Armstrong and A.P. Randall, personal communication 1969). These are only of limited use, however, because ground crews must get to the block to position the balloons. In the New Brunswick spray program, spotter or guide aircraft are employed to lead the spray aircraft through their spray patterns as shown in Figure 1, and to indicate to the pilots the appropriate "booms-on" and "booms-off" times (Irving and Webb 1981). Although this system is very effective, the observer in the spotter plane must rely on a map and his ability to recognize landmarks in the forest. Clearly, an ideal system would employ a technique that would not be affected by human error and which would not only guide the pilot to the spray block, but would ensure that the aircraft flies the appropriate pattern over the block.

The development of the Decca Navigation System seemed to provide a solution to this problem, and in 1959, it was assessed in New Brunswick (Underwood 1969). The system was effective; it guided the pilot to a plot 40 km (25 mi.) from the airstrip, and, under the Decca guidance, the aircraft flew a pattern with 200 m (656 ft) swath intervals. In the United States, the U.S.

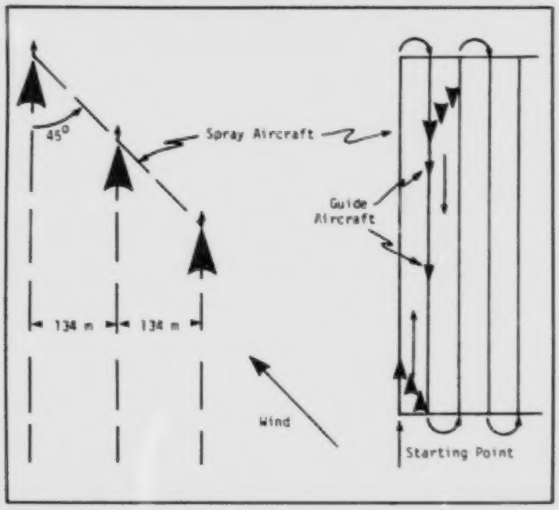

Figure 1. Diagram to show flight of spray team and position of guide aircraft in a spray block (from Irving and Webb 1981).

Department of Agriculture used the Decca system to guide spray aircraft on the fire ant control program (American Aviation 1966). This program was a success, with a very uniform pattern being flown. In a series of experimental trials in Quebec, the Decca, Global, and Litton LTN-51 navigation systems were assessed to determine their potential for operational use (Randall 1974). The Litton system was selected as the most suitable and is used to guide the 4-engined spray aircraft on the operations in eastern North America. Even with the Litton system, the Quebec authorities use twin-engined spotter aircraft flying above the spray plane to monitor the application (L. Dorais, personal communication 1984). Although effective, the Litton system is only suitable for multi-engined aircraft because of cost and operational requirements. In a report on recent developments and future needs in forest spraying, Ekblad and Barry (1977) noted that there was need for guidance systems for small aircraft, because the present systems are too expensive or too complex for a solitary spray pilot to use.

The CANUSA Spruce Budworms Program

When the CANUSA agreement was signed in 1977, forest managers were still facing the same problems that they had faced since 1950. The budworms were present in large numbers over large areas. Although newer aircraft, more effective insecticides, newer and better emission systems, guidance systems, and a better understanding of weather effects on spray cloud dispersal were available, the operations manager did not seem to be winning the battle. To the onlooker, all that was taking place was a continuing spray program that appeared to have no completion date. Operation managers and some researchers felt that the scientific community was not addressing the problem effectively. As a result, the first aim of the CANUSA program was to list identifiable targets, subtargets and activities, with completion dates and clearly stated outputs. Table 5 summarizes the goals and outputs for Target 4 "Treatment Strategies."

Achievements under the CANUSA Program

Activity 4.2.1 Complete the development and evaluation of chemical and microbial insecticides considered to have high potential.

Table 5
Activities of Target 4. Treatment Strategies

Sub-target 4.2 Chemical and microbial insecticides evaluated for safety, efficacy, and cost.
Activity 4.2.1 Complete the development and evaluation of chemical and microbial insecticides considered to have high potential.

Projected outputs
1. Pest managers' guide for use of registered insecticides.
2. New recommendations for control products, with objective of assembling registration packages for new materials expeditiously. Improved use of B.t. Efficacy data on promising materials. User guides and prescriptions for users of insecticides.
3. Information for registration of one chemical and one microbial insecticide.
4. Evaluation of currently registered and new products for western spruce budworm (WSBW) control. Efficacy data on promising materials.

Activity 4.2.2 Improve application technology to increase effectiveness of specific insecticides.

Projected outputs
1. User manuals on application technology. Prescriptions for application strategies.
2. Improved guidance for spray aircraft. Information on insecticide loss in spray trajectory.

Activity 4.2.3 Evaluate combinations of chemical and microbial insecticides.

Projected outputs
1. Evaluation of uses of combinations of insecticides and microbials. Definitive recommendations for use of acephate-B.t. combination.
2. Information to register one chemical-microbial combination.

Development of New Insecticides

In Canada the chemical insecticides that were in the process of screening and field testing were azamethiphos (Alfacron®, a CIBA-GEIGY product) and chlorpyrifos-methyl (Reldan®, a product of Dow Chemical Company). Although both of these products showed potential for use (DeBoo 1983; Zylstra and Obarymskyj 1981), in each case the parent company withdrew their interest in the forestry market and no further field trials were carried out. The insecticide permethrin had been in the screening/testing process in Canada since 1975. The product was very effective (P.C. Nigam, personal communication 1979; DeBoo 1980 a,b) at dosage rates as low as 35.0 g AI/ha (0.5 oz/acre) in a single dose or 2 × 17.5 g AI/ha (2 × 0.25 oz/acre) in double applications. But in a series of environmental studies on the effect of permethrin on the aquatic ecosystem and terrestrial anthropods, the extreme toxicity of this product was noted. (A review of this multiyear program of work is to be found in Kingsbury [1984]). This impact was noted at application rates very close to the amount required to be efficacious against the spruce budworm, and the question was raised as to its environmental impact if used operationally. In policy discussions on pesticide development, the Forest Pest Management Institute of the CFS concluded that, because of the extreme adverse impact on the aquatic ecosystem at dosages only marginally above the proposed operational dose, permethrin could not be considered for large scale operational use over forested areas. The Institute did recommend, however, that permethrin be developed for use on smaller areas such as plantations and seed orchards. It had earlier been decided that since permethrin represented the first of the new class of synthetic pyrethroids, research would continue. As a result of these decisions, an intensive program was carried out to assess permethrin impact on aquatic ecosystems, birds, and nontarget anthropods (Kingsbury 1984). The program also included efficacy studies of permethrin applied using both air and ground spray equipment in emulsions and oil solutions (DeBoo 1980 a,b) and residue studies (K.M.S. Sundaram, personal communication 1984). The Institute is continuing its research program on permethrin, and the product is now under review for registration in Canada with a use pattern restricted to plantations and areas less than 500 ha (1240 acres).

In the western United States, a project to investigate the use of acephate applied as implanted capsules to provide a systemic effect for control of the western spruce budworm has yielded interesting results (Reardon and Haskett 1981). It was found that foliage protection to grand fir and Douglas-fir was provided with an implantation rate of 1 capsule containing 0.8 g acephate per 10 cm (4 in) trunk circumference. The capsules were applied three times at two heights on the trees. Although the technique was found to be effective, concern was expressed over the effect of the implantations which resulted in discoloration of the xylem tissue. Other research in the western United States has focused on generating knowledge for a better understanding of the total impact of a spray on spruce budworm populations. Fellin (1983) studied the effects of mexacarbate on the fecundity of adult survivors of the spray; no significant effects were reported. Similarly, Parker et al. (1978) and Parker and Lessard (1979) examined the longer-term impact of aerial sprays of carbaryl on budworm populations. Their work showed that with spraying, population levels in the treated area increased slightly, but even with the increase the population level remained low. In a series of studies reported by Markin and Grimble (1979), Markin and Johnson (1979), and Markin (1983), methomyl, permethrin, carbaryl, phosmet, sulprofos, acephate, and chlorpyrifos-methyl were applied aerially to test plots in Idaho and Montana. The purpose of the tests was to compare their relative effectiveness with respect to application rates and timing. These tests showed that whereas methomyl was effective, timing was critical. Chlorpyrifos-methyl was shown to be marginally effective, reflecting the Canadian experience with this product. Acephate was tested at the reduced rate of 560g AI/ha (8 oz/acre) (normal U.S. registered rate of application 1120g AI/ha [16 oz/acre]) and shown to be effective. As a result, a new registration at this reduced rate was granted. Tests with permethrin demonstrated the efficacy of this product at 112 and 56g AI/ha (1.6 and 0.8 oz/acre). The phosmet and sulprofos trials did not provide acceptable levels of control.

The identification and testing of new forestry-use insecticides is carried out at the USDA Forest Service Laboratory at Berkeley, California, and at the Forest Pest Management Institute of the Canadian Forestry Service in Sault Ste. Marie, Ontario. A review of the change in both number and variety of compounds being tested for the period prior to the start of the CANUSA Program to the present is a matter of concern to those working in this field in that there has been a decrease in the number of new compounds being tested.

In the United States at the start of the CANUSA Program, Robertson (1975, 1976) reported the results of the assessment of 16 compounds: chlorpyrifos, chlorpyrifos-methyl, biothanomethrin, permethrin, aminocarb, mexacarbate, trichlorfon, methamidophos acephate, methomyl, phenothrin, resmethrin, pyrethrins, and pyrethrins BCD, RU 168S, and carbaryl. With carbaryl as the standard, chlorpyrifos-methyl was the most toxic with an LD_{50} approximately 100 times less than that of carbaryl. Subsequent testing (Robertson and Kimball 1979) included only nine new compounds, again with carbaryl as the standard. The insecticides tested were a series of numbered compounds: FMC 30980, 35171, 55381; M 10364, 10445, 8983, and 9420; and idinphos. In this series all materials were more toxic than carbaryl with the FMC 55381 being most toxic (1899 times more toxic at the LD_{50} level).

A similar pattern of decreasing numbers of new insecticides is seen in Canada. In the early 1970s, Nigam (personal communication 1984) tested 20-30 new compounds per year; at the start of the CANUSA Program, Nigam (personal communication 1979) reported the results of testing 12 compounds: A5675A, A41286, A47171, AC222-705, BAY 9306, azamethiphos, chlorpyrifos-methyl, permethrin, acephate, fenvalerate, cypermethrin, and SAN279. In terms of contact toxicity, azamethiphos and AC222-705 (a pyrethroid) were most effective. Chlorpyrifos-methyl was the most effective for residual toxicity, followed by cypermethrin. During the final year of the CANUSA Program only five new insecticides were tested in Canada. These were: thiodicarb, UC56295, UC72987, AC218-962, and AC217-300 (B.V. Helson, J.W. McFarlane, D,.R. Comba, personal communication 1983). Of these five, two (UC56295 and AC268-192) have been dropped by the respective parent companies.

The two products that appeared to have potential for use against the spruce budworms were chlorpyrifos-methyl and azamethiphos. The testing of these materials in Canada had progressed to the field trial stage with aerial applications to plots 50-100 ha (125-250 acres) in size (Zylstra and Obarymskyj 1981; DeBoo 1983). Unfortunately the parent companies decided to withdraw their products from the market; since that time no new insecticides have been field tested in Canada.

Development of New Formulations

A significant development that has taken place is in the formulation of insecticides. Research by Mobay-Chemagro Co. Ltd., and Union Carbide Corporation resulted in the development of "flowable" formulations. Basically these are preparations in which the insecticide is in the form of very small particles (a few microns in size) suspended in an oil. The product can be tank-mixed to give either an oil or water suspension. This is of particular advantage to carbamate insecticides which, in the oil solution formulation, crystallize out immediately on contact with water. Considerable work has been done on these formulations to improve their mixing qualities to meet the harsh requirements of an operational program, i.e., use of water at 1-3°C (34-37°F) with no heating facilities (A. Sundaram and J.W. Leung, personal communication 1983). The new aminocarb formulation was particulary successful and was equally efficacious against the spruce budworm as the oil soluble formulation (L. Cadogan, personal communication 1981). It is now registered in both the United States and Canada, and was used operationally in both countries in 1984. This registration met one of the goals of the CANUSA Program: the registration in both countries of a new insecticide (or formulation) for spruce budworm control. There has been, however, and continues to be, concern over the effects of the "non-toxic" portions of spray mixes on the forest ecosystem (Lockhart et al. 1984, Weinberger and Greenhalgh 1984). And in Canada, in the province of New Brunswick in particular, there have been concerns about the effects of the insecticides and the constituents of the tank mixes used on the budworm spray programs on human health and the environment. McLeese et al. (1980) had identified the nonylphenol portion of the aminocarb oil solution as being as toxic to fish as the aminocarb itself. Field trials with nonylphenol alone (no aminocarb) applied in insecticide diluent 585 at greater than the normal application rate experienced in an operational spray refuted this report (Holmes and Kingsbury 1979). The development of the aminocarb flowable formulation has overcome these problems and this product has been shown to be less toxic to the aquatic ecosystem than the oil soluble formulation (W.B. Ernst, personal communication 1981).

The insecticide mexacarbate which had been developed and registered by Dow Chemical Co. and which was used extensively in the United States was never widely used in Canada. This product dropped from the market and recently Union Carbide has picked up the patent from Dow. Research is now under way to develop a new formulation of this material and in 1984, field trials of Zectran DB were carried out (L. Cadogan, personal communication 1984). The new fenitrothion formulation known as Sumithion F20 was also field tested. The studies showed that both products were as effective as the original oil formulations and that the new water and oil tank mixes of the flowable were equally effective (L. Cadogan, personal communication 1984).

Development of Test Protocols

Test protocols to develop new insecticides have evolved along different lines in Canada and the United States. In Canada the mandate of the Forest Pest Management Institute is to identify and develop environmentally acceptable efficacious materials for the control and management of forest pests. The Institute has developed a multidisciplinary program involving laboratory tests to identify new products, small scale field trials to determine efficacy, environmental studies to determine the impact on the forest ecosystem (birds, small mammals, fish, aquatic and terrestrial arthropods are all studied), and chemical residue studies to measure the breakdown of the insecticide and the fate of the metabolites. These studies include foliage, litter, forest soil, water, stream sediment, and aquatic plants. At the final stage of the testing, semi-operational trials are carried out in cooperation with one of the operational programs. In these trials the operator, using normal operational protocols and standards, applies the insecticide and the Institute scientists, in cooperation with scientists from regional forestry research centres and other agencies, determine the environmental effects of the spray. This total program spans a period of about 5 years. The advantage of the multidisciplinary approach is that all aspects of spray application deposit and effect are measured and good correlations are possible; if an adverse effect occurs, changes to the formulation or application can be made.

In the United States there has been a major effort in the area of predictive modeling and the development of laboratory techniques that will indicate not only effective insecticides for field use, but also field application rates and strategies. Robertson and Haverty (1981) and Haverty and Robertson (1982) have reported studies on intrinsic toxicity, residual toxicity, and rainfastness of insecticides applied in the field. From the data they were able to determine an estimated minimum effective dose to cause 90 percent mortality (MED_{90}). These data were then correlated with the estimated effective dose to cause 90 percent mortality (ED_{90}) determined in laboratory tests. When the rainfastness quality was brought into the equation they were then able to determine the ratio of the MED_{90} to the ED_{90} and get a better approximation of the field application rate. This technique does not replace the field trial step, nor will it enable one to accurately predict the field application rate, but it should reduce the number of aerial application field tests. Further research in the area of predictive modeling (Force et al. 1982) resulted in the development of a model designed to simulate efficacy of insecticides to the Douglas-fir tussock moth and the western spruce budworm. The variables affecting the model are: insecticide dosage at the foliage-insect level, response of the insect to the insecticide, instar distribution on the day of spray, type of exposure, moisture condition of the foliage, rainfall after spray, and the presence or absence of larvae at the time of spray. The model shows that inferences based on one type of data result in misleading conclusions. The model appears to predict the mean results of field applications to within about 5 percent of the observed efficacy and has an accuracy of prediction from 73 to about 95 percent. The authors state that the model can be used as a planning device and they suggest that if used with the spray dispersion, deposition, and canopy penetration model (Dumbauld et al. 1977), it will enable the user to forecast mortality under a variety of environmental and stand conditions.

Activity 4.2.2. Improve application technology to increase effectiveness of specific insecticides.

Developments to Improve Atomization

Ekblad and Barry (1977) identified three areas of research most likely to yield significant and substantial improvements to spray operators. These were: a) nozzle development, b) aircraft guidance, and c) models for selecting optimum droplet size and appropriate meteorological conditions for application. The first budworm sprays were carried out using nozzles developed for agricultural sprays. Although these were originally considered acceptable, early work by operators such as Flieger (1953) showed that spray objectives could be achieved at reduced dosages with a properly atomized spray. Studies to compare different types of atomizers were carried out in the United States (Akesson et al. 1969) and in Canada (Randall 1975). These studies sought to characterize the drop size spectrum produced by the different nozzles and to identify nozzle types that would meet the spray operators objectives. In a review of the development of ultra low volume (ULV) spraying concepts for budworm control in Canada, Armstrong (1981) compared the work done by the Canadian Forestry Service and operators such as B.W. Flieger with that of the work done by Himel (1969), Himel and Uk (1975), and Spillman and Joyce (1978). Whereas Himel and Spillman and Joyce determined the optimum drop size and emission rate through a series of modeling, laboratory, and field studies, the Canadian workers made their selection through a series of field trials in which volume and drop size were varied. In each case the investigators come to the same result, i.e., that for spruce budworms control, small droplets (less than 50 microns) were most effective. Randall (1975) found that the Micronair® AU 3000 atomizer was ideally suited as an operational spray atomizer to produce the cloud of finely atomized droplets, and this unit (and more recently the AU 5000) has become the accepted atomizer for use in Canada and the United States on aircraft with speeds between 150 and 200 Km/hr (90 and 125 m.p.h.). More recently, the Beecomist® rotary nozzles have been field tested and found to be effective, particularly on aircraft flying at higher speeds such as the 4-engined aircraft (Armstrong 1981) or on helicopters flying at a variable speed. At the start of the CANUSA Program, the Teejet® nozzles were still being used on some aircraft, while the Micronair® AU 3000 and the Beecomist® rotary atomizers were gaining in popularity. The rotary atomizers were more effective because they produced a spray cloud with a smaller Dmax and a narrower spectrum of drop sizes than the Teejet®. In an attempt to produce a spray cloud of uniform drop size, Yates and Akesson (1980) developed the aerodynamic mono-disperse atomizer. This unit produces droplets in the 200 micron size range and although this is too large a droplet for spruce budworm control, this development indicates that technology will eventually provide the spray operators with the equipment needed to optimize spray delivery. The development of such spray atomizers, allied with the monodisperse droplet generator used in laboratory studies, gives scientists the opportunity to prescribe precise spray cloud characteristics to generate the biologically optimum droplet described by Joyce (1975).

Aircraft Guidance

Developments in electronic technology and avionics have resulted in the production of small, portable transponder units which are used to guide boats and commercial aircraft in coastal areas. These units have a high degree of accuracy — plus or minus a few metres — and have the potential for use as guidance indicators for small aircraft. The units have been field tested in the agricultural context (Yates and Akesson 1980) and were found to be accurate and effective. The units were field tested in New Brunswick on the spruce budworm spray program (H.J. Irving, personal communication 1984). The rolling and hilly terrain typical of forested areas screened out some of the signals, rendering the system ineffective. The only option to overcome this problem was to have a larger net of ground units. On the large area New Brunswick program, the sequential moving of the ground units was not practical, and with the high cost of a large number of units, the system did not have potential for use. In the province of Ontario, the Del Norte guidance system is used. It should be noted that the provincial policy is not to treat extensive outbreak areas but rather to concentrate on epicenter suppression to eliminate small defined insect epidemics; and to effect outbreak control, to contain larger infestations with protection spraying on specific areas such as provincial parks, plantations, seed orchards, and wildlife habitat (McGauley 1984). Under this policy the spray program is geared to the treatment of a number of smaller areas and the total area for treatment in any one year is normally between 5 000 and 10 000 ha (12,000 and 25,000 acres). This is in direct contrast to the large area programs in Maine, New Brunswick, and Quebec. With smaller spray blocks requiring treatment the standard agricultural spray aircraft is used in Ontario. Under these conditions, ground-based systems such as marker balloons, good maps, and aerial photographs associated with intensive pilot briefings form the most common means of guidance. The pilot then flies on his own to the block and is responsible for the application under the supervision of a spotter aircraft. The Ontario provincial authorities have investigated the use of the Loran system but because of the lack of appropriately placed ground units to serve Northern Ontario, this system could not provide the required degree of accuracy. The Del Norte system has proved to be very effective (S.A. Nicholson, personal communication 1984). The unit is mounted in a Cessna 172 which acts as a lead aircraft to the spray plane flying in echelon. With the smaller blocks the ground-based transmitters can be located to provide appropriate coverage. The province has used this guidance system for 3 years; although it is very expensive, its accuracy (±3m of desired flight track) has justified its use. In Maine where a mixture of large and small spray aircraft are used, the Litton system for the large aircraft and spotters for the ag-type spray planes are employed.

Spray Cloud Modeling

During the CANUSA Program there have been significant advances in modeling spray cloud behavior. Following the work of Cramer and Boyle (1976) in which the different processes affecting droplet transport, diffusion, and deposition were enunciated, the USDA Forest Service expanded its studies in this area. Dumbauld (1984) has reviewed the work done and indicated some of the models that must be considered for a complete program. The models include aircraft wake, droplet evaporation, dosage, concentration, and deposition and canopy penetration. The Cramer, Barry, Grim model — referred to as CBG — has been used by the USDA Forest Service to predict spray cloud behavior above and within forest canopies (Dumbauld et al. 1977). A field comparison of this model was carried out in a spray trial at the Withlacoochee State Seed Orchard (Rafferty et al. 1981). Although such problems as accounting for the effects of the wake from the low-flying spray aircraft and droplet sizing were encountered, the test did demonstrate the usefulness of the model to assist in the planning and implementation of an aerial application.

Prior to the CANUSA Program, very little work had been done on modeling of spray cloud behavior in Canada. Most spray operations were carried out under what were considered "the best" spray conditions, i.e., a wind speed less than 16 km/hr (10 m.p.h.), and under a temperature inversion (Armstrong 1975). In fact, these were the guidelines that the province of New Brunswick laid down for permissible spraying (H.J. Irving, personal communication 1984). These conditions are normally found only in the early morning and late evening, and as a result, spray operations were limited to a few hours a day. The work of spray modelers, such as Cramer, Barry, and Dumbauld in the United States (Dumbauld et al. 1977; Dumbauld 1984), Bache (1975) and Spillman and Joyce (1978) in England, and Picot and Kristmanson (1975) in Canada, produced data to show that sprays could and should be applied under turbulent conditions. These spray conditions resulted in less drift and better droplet impaction and, from the operators viewpoint, extended the number of usable hours per day. The spray cloud modeling efforts were expanded in the United States and in Canada. Under the stimulus of Forest Protection Limited, a more active modeling program was initiated (Irving and Webb 1981). In a collaborative program involving the National Research Council Canada, University of New Brunswick, Atmospheric Environment Service, and the New Brunswick Research and Productivity Council, models were developed and field tested (Wiesner 1984). The findings of this program showed that measurable amounts of fenitrothion could be found in the atmosphere at up to 80 km (50 mi.) from the spray area (Crabbe et al. 1980) and that, under the classical spray weather conditions, there was more drift in the mid- to long-range distances than under neutral to slightly unstable conditions (Crabbe et al. 1980, 1984).

Associated with the research to determine most effective application rates, is the need to determine the amount and characteristics of the spray deposit. Hurtig et al. (1953) developed the technique of using Kromekote® cards placed on the ground and relating the deposit on these surfaces with the mortality in the tree. Maksymiuk (1963a, 1963b) found that with cards correctly placed it was possible to obtain a good correlation between the deposit and insect kill. Armstrong and Randall (1969) also used this sampling technique as did researchers in the United States (Young 1978, Flavell et al. 1977, Williams and Robertson, 1983).

Activity 4.2.3. Evaluate combinations of chemical and microbial insecticides.

The concept of using a microbial control agent with a chemical insecticide has always intrigued scientists. The rationale for this philosophy is that many microbial insecticides, while effective, are slow acting, and it is felt that if the correct mix or correct sequence of treatment could be developed it might be possible to achieve the quick kill of a chemical insecticide with the environmental safety of the microbial. In studies in Canada, Morris et al. (1974) assessed the long term effects of a treatment with fenitrothion (applied at 17.5 g AI/ha [0.25 oz/acre]: normal treatment 210 g AI/ha [3 oz/acre]) followed by treatment of nuclear polyhedrosis virus (NPV) or entomopox virus (EPV). The study, carried out over a 2-year period, showed that the combination of NPV and fenitrothion or EPV and fenitrothion had a greater immediate impact in terms of larval population reduction and a greater long-term impact than did either the fenitrothion or virus treatments alone. The NPV and fenitrothion combination was more effective than that of EPV and fenitrothion. An assessment of this application 3 years after treatment (Morris 1977a) showed that the NPV and fenitrothion treatment was still affecting the budworm population. This was caused by the transmission of the virus to succeeding generations and was seen as a decrease in damage to balsam fir. In studies on the effects of mixtures of chemical insecticides and B.t., Morris and Armstrong (1975) and Morris (1977b) used mixes of B.t. and acephate and B.t. and fenitrothion compared with B.t. alone. The chemical insecticides were applied at much less than normal registered rates: acephate was used at 21, 42, and 63 g AI/ha (0.3, 0.6, and 0.9 oz/acre) (registered rate 560 to 1120 g AI/ha [8 to 16 oz/acre]) and fenitrothion was used at 17.5 g AI/ha (0.25 oz/acre) (registered rate 210-280 g AI/ha [3-4 oz/acre]). The sprays of B.t. and chemical insecticide compared favorably with the treatments of chemical insecticides alone at the full registered rate. Dimond and Spies (1980) assessed the effect of a B.t. and acephate mix in aerial applications in Maine. Their trials did not achieve the same degree of effectiveness as did those of Morris and Armstrong (1975). Morris (1975, 1977c) had studied the effects of chemical insecticides on, and their compatibility with B.t. One of his findings was that there was a dose effect of the chemical insecticide on the B.t. and it was for this reason that the low rates of acephate and fenitrothion were used in his trials. Dimond and Spies (1980) had used acephate at the registered rate, and possibly this higher rate of application was one reason for their lack of success.

Silk and Kuenen (1984), in their review on the use of pheromones, comment on studies done in New Brunswick in which pheromones were used as a lure to attract males to an insecticidal trap. Although laboratory studies had shown the technique to have potential, field trials did not yield the same degree of success. Apparently, although mixtures of microbial and chemical insecticides or pheromone plus insecticide are very interesting scientifically, they are either unacceptable or unworkable operationally.

The use of mixtures of chemical insecticides has long been used for control of flying insects, the well-known pyrethrin and DDT spray being probably the best known example (Brown 1951). These mixes with their synergistic effect were very effective and useful. The technique is now being evaluated for spruce budworms control. Robertson and Smith (1984) have reported on their work in this area. Three pyrethroids (decamethrin, fenvalerate, and permethrin) were mixed with four carbamates (aminocarb, carbaryl, methomyl, and thiodicarb) and five organophosphorous insecticides (acephate, chlorpyrifos, fenitrothion, malathion, and phosmet). The mix ratios were 1:10. The mixtures were applied topically to sixth instar larvae of the western spruce budworm. The criterion for a synergistic effect was the occurrence of a significantly greater mortality than could be expected from a model of independent uncorrelated action as described by Robertson and Smith (1984). Based on this criterion, Table 6 summarizes the results of the tests.

The concept of using sequential mixtures of insecticides had been explored in Canada (H.J. Irving, personal communication 1984) as a consequence of concern over the necessity for multiple applications to combat very high budworm populations in areas where the trees were stressed from previous severe defoliation. The concern was that two treatments of fenitrothion might cause an adverse impact on birds and the environment. The aim was to use aminocarb and fenitrothion in that sequence, or the reverse. In the province of New Brunswick this technique was used until 1976; however, at that time, the provincial health authorities expressed concern over the possible harm to the local population from the use of these combinations and their different solvents. The provincial government adopted the policy of using a single chemical insecticide (H.J. Irving, personal communication 1984). The province of Quebec also explored the use of sequential treatments of aminocarb and fenitrothion, and Ontario used B.t. and acephate as an operational tool for a few years. Like New Brunswick, these provinces have reverted to the single insecticide philosophy. It would thus appear that, as a result of the desire to generally restrict chemical insecticides in favor of microbials and the desire to use only a single compound in an area, authorities are not willing to support the use of combinations of insecticides.

Conclusion

The first aerial spray program against the spruce budworm took place in 1949. At that time entomologists indicated that the only suitable time for insecticide application was the later larval instars. Today, 35 years later, the spray programs are still aimed at the latter instar larvae or at the stage of shoot development at which the bud cap has been shed and the shoot has started to flare to give the open shoot. This is not to be taken as an adverse comment on the lack of progress in the area of timing of insecticide application, but rather an indication that to meet the goals of spruce budworm population management and foliage protection, this is the best time for treatment. The actual aerial application technique has not changed much. Larger aircraft capable of treating larger areas on a single flight are being used, but for smaller areas the agriculture spray plane is the standard aircraft. There have been significant changes in spray atomization equipment, yet again, on many operations, standard hydraulic nozzles are still used.

After 35 years of operational spraying and intensive research in both the United States and Canada, we are still seriously limited in the number of insecticides available for budworms control. Although the list of registered products may seem impressive — 7 chemicals and 1 biological in Canada; 10 chemicals and 1 biological in the United States; there have been only 2 chemicals — (aminocarb and fenitrothion) used widely in Canada and 2 chemicals (carbaryl, acephate) used extensively in the United States in the past few years.

At the initiation of the CANUSA Program there was much discussion about the objectives identified and the possibility of attaining them. The formal CANUSA agreement is now completed; we have had annual reports during the past 5 years and we have, during the course of this symposium, listened to a series of presentations and seen the poster displays outlining the work completed. From these, two facts become apparent: a) some of the goals were achieved and the results of the work are now being implemented, and b) of the goals not achieved, we must ask ourselves whether they were attainable from a scientific/technical standpoint, whether the time frame was too short, or whether resources were too limited.

Research to complete the development and evaluation of new insecticides, whether biological or chemical, must continue. During the course of the CANUSA agreement no new chemical insecticides were registered. Aminocarb had been used operationally over several million hectares (acres) in Canada as a registered insecticide, and over more than 1000 ha (2,500 acres) as an experimental compound in the State of Maine. The major development with aminocarb was the new flowable formulation which gave the operator the opportunity of applying it either as an aqueous or as an oil suspension. This formulation is now registered in both the United States and Canada. Acephate had been used before the CANUSA agreement; although it is an ideal compound for use near streams because of its low toxicity to fish, concern about its safety to birds and lack of rainfastness has resulted in limited use of this product. The large operations in the eastern United States and Canada have relied heavily on fenitrothion, aminocarb, and carbaryl and until new products appear, these will continue to be the major chemical insecticides for operational use.

Table 6
Incidences of synergism with 1:10 mixes of synthetic pyrethroids with selected carbamate and organophosphorous insecticides

	Decamethrin	Fenvalerate	Permethrin
aminocarb	0[1]	+[2]	0
carbaryl	+	+	+
methomyl	0	+	+
thiodecarb	0	+	+
acephate	+	+	0
chlorpyrifos	+	0	0
fenitrothion	+	+	0
malathion	0	0	0
phosmet	0	+	0

[1] no synergism or an antagonistic effect (reduced mortality).
[2] synergism.

The significant change in chemical insecticides that has occurred is the development of new formulations. We now have the flowable formulation of aminocarb, and new formulations of mexacarbate and fenitrothion are being studied at the Forest Pest Management Institute. If these products prove to be successful, and become registered, the forest manager will have compounds that can be tank-mixed easily and applied either as a water-base or as an oil-base spray. There is concern that these are the only developments in the field of chemical insecticides. Researchers have noted the lack of new products for screening: as an example, in Canada in the 1970s approximately 20-30 new compounds entered the screening program each year (P.C. Nigam, personal communication 1984), whereas in the last 2 years only 2-3 new compounds have been identified (B.V. Helson, personal communication 1984).

The development of biological insecticides has been reviewed by Cunningham (1985). The recent success with *Bacillus thuringiensis* in the development of the high concentrate formulations that can be applied at low volume rates of 2.5 L/ha (0.25 gal/acre) has significantly affected spray programs. This low-volume emission rate, combined with research on optimum drop size for maximum effect, has resulted in a spray that is not only effective but more economically competitive with chemical insecticides. The change in utilization is dramatic, and as a result, in Canada operational use of B.t. has increased from about 60 000 ha (150,000 acres) up to the year 1983 to more than 400 000 ha (1 million acres) in 1984. This change is from an average of approximately 2.5 percent to over 25 percent of the total Canadian budworm program.

Research on drop size specificity for optimum effectiveness, allied with studies on spray cloud behavior, must be continued. Concern over the general inefficiency of aerial spray applications and the impact of off-target drift of the spray cloud has seriously hindered spray operations. Until such time as the "targeting" of the spray cloud can be improved, operators will be severely restricted through the imposition of buffer zones and set-back areas from carrying out an efficient spray. These spray clouds of specific drop sizes will only become a reality when the operators have spray nozzles that will produce the required droplets.

A final and very important area of research is the development of guidance systems suitable to forestry operations. The guidance systems presently available are either too expensive to use relative to the cost of the aircraft, or ineffective in the rolling to mountainous terrain of our forested regions.

As more effort is directed towards forest management, so will more effort be directed towards insect control. Although we all look forward to the day of the "perfect" biological control, we must still acknowledge that chemical insecticides will continue to play an important role. Integrated pest management will be practiced even more than it is today with the judicious use of chemicals and biologicals as required to meet management objectives. The manager will, as A.W.A. Brown said in 1951, "use insecticides as a stilleto rather than a scythe."

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Literature Cited

Akesson, N.B., Yates, W.E.; Wilce, S.E. 1969. Performance of atomizers for aircraft chemical applications. Pages 254-264 *in* Proc. Fourth Int. Agric. aviat. Congr. (Kingston).

American Aviation. 1966. Decca system looks good for large scale Ag. Operations. American Aviation. Aug. 1966. 4p.

Armstrong, J.A. 1975. Forest meteorological conditions and spray deposition. Pages 169-176 *in* Proc. Fifth Int. Agric. aviat. Congr. (Warwickshire).

Armstrong, J.A. 1977. Relationship between the rates of pesticide application and the quantity deposited in the forest. Pages 193-202 *in* Proc. Symp. Fenitrothion: The long-term effects of its use in forest ecosystems (Ottawa, 1977). NRCC No. 16073.

Armstrong, J.A. 1981. ULV/CDA optimum spray droplet size for control of the eastern spruce budworm in Canada. Outlook on Agriculture 10(7):327-332.

Armstrong, J.A.; Randall, A.P. 1969. Determination of spray distribution patterns in forest applications. Pages 196-202 *in* Proc. Fourth Int. Agric. aviat. Congr. (Kingston).

Armstrong, J.A.; Yule, W.N. 1978. The distribution of aerially-applied spray deposits in spruce trees. Can. Entomol. 110:1259-67.

Bache, D.H. 1975. A new approach to predicting atmospheric transport of particulates. Pages 252-258 *in* Proc. Fifth Int. Agric. aviat. Congr. (Warwickshire).

Balch, R.E.; Webb, F.E.; Fettes, J.J. 1955/56. The use of aircraft in forest insect control. Forestry Abstracts 16(4), 17(1) and (2). Contribution No. 224, Forest Biology Division, Science Service, Dept. of Agriculture, Ottawa, Canada. 31p.

Barry, J.W.; Ciesla, W.M.; Tysowsky, M. Jr.; Ekblad, R.B. 1977. Impaction of insecticide particles on Western spruce budworm larvae and Douglas fir needles. J. Econ. Entomol. 70(3):387-388.

Barry, J.W.; Ekblad, R.B. 1978. Deposition of insecticide drops on coniferous foliage. Trans. A.S.A.E. 21(3):438-9, 440-1.

Barry, J.W.; Ekblad, R.B.; Markin, G.P.; Trostle, G.C. 1978. Methods for sampling and assessing deposits of insecticidal sprays released over forests. U.S. Dept. Agric., Washington, D.C. Tech. Bull. 1596. 162p.

Barry, J.W.; Wong, J.; Kenny, P.A. 1980. Deposition of pesticide droplets resulting from aerial application to conifers. Paper presented to Entomol. Soc. America Symp. "Pesticide spray application: A perspective on accountability," Atlanta, GA. Dec. 1980: 10p.

Blais, J.R. 1981 Recurrence of spruce budworm outbreaks for 200 years in Western Quebec. For. Chron. 57(6):273-275

Brooks, F.A. 1947. Dynamic catch of aerosols by obstructions. Agric. Eng. 28:233-238.

Brown, A.W.A. 1951. Insect Control by Chemicals. John Wiley and Sons, New York. 817p.

Common Names for Pest Control Products. 1980. Canadian Standards Association 2143-1980. Canadian Standards Association, Rexdale, Ont.

Crabbe, R.S.; Krzymien, M.; Elias, L.; Davie S. 1980. New Brunswick spray operations: measurement of atmospheric fenitrothion concentrations near the spray area. National Research Council Canada, Ottawa, Ont. Report LTR-UA-56.

Crabbe, R.S.; McCooeye, M.; Elias, L. 1984. Effect of atmospheric stability on wind drift in aerial forest spray trials. Neutral to stable conditions. National Research Council of Canada, Ottawa, Ont. Report LTR-UA-73: 32p.

Cramer, H.E.; Boyle, D.G. 1976. The micrometeorology and physics of spray particle behavior. Pages 27-39 *in* Pesticide Spray Application, Behavior, and Assessment. Workshop Proceedings, U.S. Dep. Agric., For. Serv., Pac. Southwest For. and Range Exp. Stn., Berkeley, CA. Gen. Tech. Rep. PSW-15/1976.

Cunningham, J.C. 1985. Biorationals for control of spruce budworms. Pages 320-349 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp. 16-20 Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

De Boo, R.F. 1980a. Experimental applications of permethrin by mist blower for control of spruce budworm in Quebec, 1975-78. Can. For. Serv., Ottawa, Ont. Bi-monthly Res. Notes 36(5):23-24.

De Boo, R.F. 1980b. Experimental aerial applications of permethrin for control of *Choristoneura fumiferana* in Quebec, 1976-1977. Can. For. Serv., For. Pest Manage. Inst. Inf. Rep. FPM-X-41. 24p.

De Boo, R.F. 1983. Efficacy of chlorpyrifos methyl for control of spruce budworm *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae) B.C. Min. of Forests, Protection Branch, Forest Service, Victoria, B.C. Internal Report PM-PB-7: 18p.

Dewey, J.E.; Ciesla, W.M.; McGregor, M.D. 1971. The 1971 western spruce budworm pilot test — Nezperce National Forest and State of Idaho Lands. U.S. Dep. Agric., For. Serv., Northern Region, Div. State and Private Forestry, Missoula, MT. 20p.

Dimond, J.B.; Spies, C.J. 1980. A comparison of B.t. plus the additives chitinase and Orthene in control of eastern spruce budworm. Maine Life Sciences and Agriculture Experiment Station. University of Maine at Orono, ME. Misc. Rep. 224. 15p.

Dumbauld, R.K. 1984. Modeling of aerial spray drift and canopy penetration. Pages 153-174 *in* W.Y. Garner, and J. Harvey Jr., eds. Chemical and biological controls in forestry. American Chemical Society, Washington, D.C. Symposium Series 238.

Dumbauld, R.K.; Rafferty, J.E.; Bjorklund, J.R. 1977. Prediction of spray behavior above and within a forest canopy. Special Report Under Contract No. 19-276. U.S. Dep. Agric., For. Serv., Pacific N.W. Forest and Range Experiment Station, Portland, OR.

Ekblad, R.B.; Barry, J.W. 1977. Forest spraying: recent developments and future needs. ASAE. 1977 Winter meeting. 13-16 Dec. 1977. Chicago, Ill. 3p.

Fellin, D.G. 1983. Chemical insecticides vs the Western spruce budworm: After three decades, What's the score? Western Woodlands 9.(1):8-12.

Fettes, J.J. 1960. Forest aerial spraying — dosage concepts and avoidance of hazard to fish and wildlife. Pages 924-929 *in* Proc. Fifth World For. Congress (1960). Vol. 2, 1962. Buenos Aires, Argentina.

Flavell, T.H.; Tunnock, S.; Meyer, H.E. 1977. A pilot project evaluating trichlorfon and acephate for managing the Western spruce budworm, *Choristoneura occidentalis* Freeman, Helena National Forest, Montana. 1976. U.S. Dep. Agric., For. Serv. Northern Region. Forest Insect and Disease Management. Report No. 77-16. 49p.

Flieger, B.W. 1953. Spruce budworm spraying in New Brunswick, 1953. Bi-mon. Prog. Report, For. Biol. Div., Dept. Agric. Can., Ottawa. 9(5):1-2.

Force, J.E.; Robertson, J.L.; Stock, M.W.; Williams, C.B. 1982. Probability model of insecticide efficacy for Western Spruce Budworm (Lepidoptera: Tortricidae) and Douglas-fir Tussock Moth (Lepidoptera: Lymantriidae). Env. Entomol. 11(6):1170-1171.

Haverty, M.I.; Robertson, J.L. 1982. Laboratory bioassays for selecting candidate insecticides and application rates for field tests on the Western Spruce Budworm. J. Econ. Entomol. 75(2):179-182.

Himel, C.M. 1969. The optimum size for insecticide spray droplets. J. Econ. Entomol. 62(4):919-925.

Himel, C.M.; Moore, A.D. 1967. Spruce budworm mortality as a function of aerial spray droplet size. Science. 156:1250-1251.

Himel, C.M.; Uk, S. 1975. The biological optimum spray droplet size. Pages 234-241 *in* Proc. Fifth Int. Agric. aviat. Congr. (Warwickshire).

Holmes, S.B.; Kingsbury, P.D. 1980. The environmental impact of nonylphenol and the Matacil® formulation. Part I: Aquatic ecosystems. Can. For. Serv., For. Pest Manage. Inst. Info. Rep. FPM-X-35.

Hurtig, H.H.; Fettes, J.J.; Randall, A.P.; Hopewell, W.W. 1953. A field investigation of the relation between the amount of DDT spray deposited, the physical properties of the spray and its toxicity to larvae of the spruce budworm. Can. Def. Res. Board. Suffield Rep. No. 176. 41p.

Irving, H.J.; Webb, F.E. 1981. Forest protection against spruce budworm in New Brunswick. Pulp and Paper Canada. Jan (1981):3-8.

Johansen, D.A. 1913. Spruce budworm and spruce leaf miners. Maine Agr. Exp. Sta. Bull. 210.

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of western spruce budworm in the American northern Rocky Mountain area, 1922-1971. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Sta. Ogden, UT. Gen. Tech. Rep. INT-20. 144p.

Joyce, R.J.V. 1975. Sequential aerial spraying of cotton at ULV rates in the Sudan Gezira as a contribution to synchronised chemical application over the area occupied by the pest population. Pages 47-54 *in* Proc. Fifth Int. Agric. aviat. Congr. (Warwickshire).

Kenaga, E.G.; End, C.S. 1974. Commercial and experimental organic insecticides (1974 Revision) Bull. Entomol. Soc. America. Spec. Publ. Oct. 1974 74(1): 77p.

Kingsbury, P.D. 1984. Environmental impact assessment of insecticides used in Canadian forest. Pages 365-376 *in* W.Y. Garner and J. Harvey Jr., eds. Chemical and biological controls in forestry. American Chemical Society, Washington, D.C. Symposium Series 238.

Latta, R.L.D.; Anderson, E.E.; Rogers, E.E.; LaMer, V.K.; Hockberg, S.; Lauterbeck, H.; Johnson, I. 1947. The effect of particle size and velocity of movement of DDT aerosols in a wind tunnel on the mortality of mosquitos. J. Wash. Acad. Sci. 37(11):397-407.

Lejeune, R.R. 1975. Western black-headed budworm. Pages 159-166 *in* M.L. Prebble, ed. Aerial control of forest insects in Canada. Can. For. Serv., Ottawa, Ont. Cat. No. FO 23/19/1975.

Lockhart, W.L.; Metner, D.A.; Billech, B.N.; Rawn, G.P.; Muir, D.C.G. 1984. Bioaccumulation of some forestry pesticides in fish and aquatic plants. Pages 297-315 *in* W.Y. Garner and J. Harvey Jr., eds. Chemical and biological controls in forestry. American Chemical Society, Washington, D.C. Symposium Series 238.

Maksymiuk, B. 1963a. Screening effects of the nearest tree on aerial spray deposits recovered at ground level. J. For. 61:142-144.

Maksymiuk, B. 1963b. Spray deposit on oil-sensitive cards and spruce budworm mortality. J. Econ. Entomol. 56:456-457.

Maksymiuk, B.; Neisess, J.; Wave, R.A.; Orchard, R.D. 1975. Distribution of aerially applied mexacarbate in a coniferous forest and correlation with mortality of *Choristoneura occidentalis* (Lepidoptera: Tortricidae). U.S. Dep. Agric., For. Serv., Pacific N.W. For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-79:196-200.

Markin, G.P. 1983. Western spruce budworm control with three dosages of Orthene, 1976. Insect. and Acaricide Tests 2:115.

Markin, G.P.; Grimble, D.G. 1979. Western spruce budworm control with three dosages of Reldan, 1977. Insect. and Acaricide Tests 4:175-6.

Markin, G.P.; Johnson, D.R. 1979. Western spruce budworm control with Lannate, 1978. Insect. and Acaricide Tests. 4:176.

McGauley, B. 1984. Presentation to symposium: Microbial control of spruce budworm and gypsy moths. Discussion panel — Formulation and Application of microbials for spruce budworms and gypsy moth control. Co-chairmen J.A. Armstrong, W.G. Yendol. Windsor Locks, Conn. April 10-12, 1984.

McLeese, D.W.; Zitko, V.; Metcalfe, C.D.; Sargeant, D.B. 1980. Lethality of aminocarb and the components of the aminocarb formulation to juvenile Atlantic salmon, marine invertebrates and a fresh-water clam. Chemosphere. 9(2):79-82.

Morris, O.N. 1975. Effect of some chemical insecticides on the germination and replication of commercial *Bacillus thuringiensis*. J. invert. Path. 26:199-204.

Morris, O.N. 1977a. Compatibility of 27 chemical insecticides with *Bacillus thuringiensis* var. *Kurstaki* Can. Entomol. 109:855-864.

Morris, O.N. 1977b. Long-term effects of aerial applications of virus-fenitrothion combinations against the spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae) Can. Entomol. 109:9-14.

Morris, O.N. 1977c. Long-term study of the effectiveness of aerial applications of *Bacillus thuringiensis* acephate combinations against the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 109:1239-1248.

Morris, O.N.; Angus, T.A.; Smirnoff, W.A. 1975. Field trials of *Bacillus thuringiensis* against the spruce budworm, 1960-1973. Pages 129-133 *in* M.L. Prebble, ed. Aerial control of forest insects in Canada. Can. For. Serv., Ottawa, Ont. Cat. No. FO 23/19/1975.

Morris, O.N.; Armstrong, J.A. 1975. Preliminary field trials with *Bacillus thuringiensis* — chemical insecticide combinations in the integrated control of the spruce budworm *Choristoneura fumiferana* (Lepidoptera – Tortricidae). Can. Entomol. 107:1281-1288.

Morris, O.N.; Armstrong, J.A.; Howse, G.M.; Cunningham, J.C. 1974. A 2-year study of virus-chemical insecticide combination in the integrated control of the spruce budworm *Choristoneura fumiferana* (Tortricidae: Lepidoptera). Can. Entomol. 106:813-824.

Morrison, T.A.; Dimond, J.B. 1978. Field trials for control of spruce budworm in Maine; A history and bibliography. Maine Dept. of Conservation Bureau of Forestry, Augusta, ME. Entomology Division Tech. Rep. No. 6. 13p.

Nigam, P.C. 1975. Chemical Insecticides. Pages 8-24 *in* M.L. Prebble, ed. Aerial control of forest insects in Canada. Can. For. Serv., Ottawa, Ont. Cat. No. FO 23/19/1975.

Parker, D.L.; Acciavatti, R.E.; Lessard, E.D. 1978. Western spruce budworm suppression and evaluation using carbaryl, 1977. U.S. Dep. Agric., For. Serv., Albuquerque, NM. Prog. Rep. No. 1, R-3 78-11. 136p.

Parker, D.L.; Lessard, E.D. 1979. Western spruce budworm suppression and evaluation project using carbaryl, 1978. U.S. Dept. Agric., For. Serv., Albuquerque, NM. Prog. Rep. No. 2. R-3.

Picot, J.J.C.; Kristmason, D.D. 1980. Aerial spraying of coniferous forests — a model for dispersion and deposition. Pages 298-311 *in* Proc. Sixth Int. Agric. aviat. Congr. (Turin).

Potts, S.F. 1958. Concentrated spray equipment. Dorland Books, Caldwell, N.J. 598p.

Prebble, M.L. 1975. Aerial Control of Forest Insects in Canada. Can. For. Serv., Ottawa, Ont. Cat. No. FO-23/19/1975. 330p.

Rafferty, J.E.; Dumbauld, R.K.; Flake, H.W.; Barry, J.W.; Wong, J. 1981. Comparison of modeled and measured deposition for the Withlacoochee spray trials. U.S. Dep. Agric., For. Serv., FPM Methods Applications Group, Davis, CA. Report No. 81-3: 39p. & Appendices.

Randall, A.P. 1974. Changing concepts and technology for the control of the spruce budworm in Canadian forests following the introduction of ULV treatments. Pages 152-165 *in* Br. Crop. Prot. Counc., Bristol. Monogr. No. 11.

Randall, A.P. 1975. Field evaluation of the Litton LTN-51 Inertial Guidance System, multi-engine spray aircraft and incremental spraying for the dispersal of liquid insecticides for the control of the spruce budworm *Choristoneura fumiferana* (Clem.) Pages 336-349 *in* Proc. Fifth Int. Agric. aviat. Congr. (Warwickshire).

Reardon, R.C.; Haskett, M.J. 1981. Effect of Orthene medicaps on populations of western spruce budworm on grand fir and Douglas-fir. J. Econ. Entomol. 74(3):266-270.

Robertson, J.L. 1975. Feeding tests of insecticides. Insecticide and Acaracide Tests 3: 145.

Robertson, J.L. 1976. Laboratory tests of insecticides on western spruce budworm. Insecticide and Acaracide Tests 3: 145.

Robertson, J.L.; Haverty, M.I. 1981. Multiphase laboratory bioassays to select chemicals for field-testing on the western spruce budworm. J. Econ. Entomol. 74(2):148-153.

Robertson, J.L.; Kimball, R.A. 1979. Toxicities of topically applied insecticides to western spruce budworm. Insecticide and Acaracide Tests 5: 203.

Robertson, J.L.; Smith, K.C. 1984. Joint action of pyrethroids with organophosphorus and carbamate insecticides applied to western spruce budworm (Lepidoptera: Tortricidae). J. Econ. Entomol. 77(1):16-22.

Silk, P.J.; Kuenen, L.P.S. 1984. Sex pheromones and their potential as control agents for forest lepidoptera in Canada. Pages 35-47 *in* W.Y. Garner and J. Harvey, Jr., eds. Chemical and biological controls in forestry. American Chemical Society, Washington, D.C. Symposium Series 238.

Snowden, P.; Andrews, W.E.; Saufley, G. 1977. Spray deposit distribution within balsam fir crown. Evaluation Report P-77-6. U.S. Dep. Agric., For. Serv., NA Area, S & PF, Upper Darby, PA: 8p.

Spillman, J.J.; Joyce, R.J.V. 1978. Low-volume and ultra low-volume spray trials over Thetford Forest. Pages 13-24 *in* Control of Pine Beauty Moth by fenitrothion in Scotland, 1978. Forestry Commission, Alice Holt Res. St., Farnham, England.

Spray Deposit Assessment Workshop, 1976. U.S. Forest Service. FIDM-Methods Application Group, USDA Expanded Douglas-fir Tussock Moth Program, USDA Expanded Gypsy Moth Program. Davis CA. 33p.

Underwood, D.J. 1969. The contribution of avionics. Pages 121-127 *in* Proc. Fourth Int. Agric. aviat. Congr. (Kingston).

Weinberger, P.; Greenhalgh, R. 1984. Ecotoxicity of adjuvants used in aerial spraying. Pages 351-363 *in* W.Y. Garner and J. Harvey Jr., eds. Chemical and biological controls in forestry. American Chemical Society, Washington, D.C. Symposium Series 238.

Weisner, C.J. 1984. Droplet deposition and drift in forest spraying. Pages 139-151 *in* W.Y. Garner and J. Harvey, Jr., eds. Chemical and biological controls in forestry. American Chemical Society, Washington, D.C. Symposium Series 238.

Williams, C.B. Jr.; Robertson, J.L. 1983. Spray volume measurement as an interface between laboratory and field efficacy data. J. Econ. Entomol. 76(2):215-218.

Worthing, C.R., ed. 1979. The pesticide manual: a worldwide compendium. British Crop Protection Counc. 6th ed. The Boots Co., Nottingham, England. 655p.

Yates, W.E.; Akesson, N.B. 1980. Design and evaluation of pulsed jet spray systems for agricultural aircraft. Pages 345-364 *in* Proc. Sixth Int. Agric. aviat. Congr. (Turin).

Yates, W.E.; Akesson, N.B. 1980. Evaluation of a transponder type swath guidance system. Pages 139-151 *in* Proc. Sixth Int. Agric. aviat. Congr. (Turin).

Young, R. 1978. Deposit/mortality data analysis. Pages 119-128 *in* J.W. Barry, R.B. Ekblad, G.P. Markin and G. Trostle, eds. Methods for sampling and assessing deposits of insecticidal sprays released over forests. U.S. Dept. Agric., Washington, D.C. Tech. Bull. No. 1596. 162 p.

Zylstra, B.F.; Obarymskyj, A. 1981. Experimental aerial applications of permethrin, carbaryl and chlorpyrifos-methyl for control of eastern spruce budworm, *Choristoneura fumiferana* Clem. in New Brunswick in 1980. Can. For. Serv., For. Pest Manage. Inst., Inf. Rep. FPM-X-56. 14p.

Biorationals for Control of Spruce Budworms

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In this review, the term biorationals includes all methods of spruce budworm control, except cultural control, which do not involve the use of broad spectrum chemical pesticides. Because of its economic importance, a great deal of research has been conducted on spruce budworm (*Choristoneura fumiferana*) to find innovative and environmentally acceptable control strategies. However, it is a difficult candidate because of the vast areas infested and because of immigration from untreated to treated areas. Less research has been conducted on western spruce budworm (*C. occidentalis*), which occurs in isolated pockets.

The ideal solution for insect pest regulation involves the release of a self-replacing organism, such as a parasite or pathogen, which establishes in the population, spreads to untreated areas and reduces the population to an endemic level. Such a technique has not been found for spruce budworm and all agents currently used are applied in the same way as chemical pesticides. They affect only the treated generation.

A bacterium, *Bacillus thuringiensis* (B.t.), is the only biorational agent produced commercially and registered for spruce budworm control. Its performance has improved greatly in recent years with the introduction of high potency formulations applied at low volumes. B.t. is now a viable alternative, in terms of both cost and efficacy, to chemical pesticides and its use is increasing. Viruses are expensive to produce and none has caused major epizootics, fungi have not been developed to the stage of aerial spray trials and protozoa are considered poor candidates for development. No successes have been recorded following the release of exotic parasites, but there is interest in inundative releases of the egg parasite, *Trichogramma minutum*. Only preliminary tests have been conducted with entomopathogenic nematodes and an effective formulation remains to be found for forest applications.

Some moult inhibitors have shown considerable promise in field trials on spruce budworm and may soon be available commercially. The use of sex pheromones for mating disruption requires further research and may not be practical for suppression of epidemic populations. Research on antifeedants is at a preliminary stage. Some consideration has been given to the release of sterile males, but this strategy is not being pursued.

New techniques of genetically manipulating micro-organisms show great promise for enhancing the efficacy of B.t. and viruses for spruce budworm control. This line of research is being actively pursued, and hopefully, new and improved products will become available for field testing.

Dans la présente étude, sont dites biologiques toutes les méthodes de lutte contre la tordeuse, sauf les méthodes culturales, qui n'exigent pas l'utilisation de pesticides chimiques à spectre large. À cause de l'importance économique de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana*), une grande partie de la recherche a porté sur cet insecte afin de trouver des méthodes nouvelles et écologiques de lutte. Toutefois, la

difficulté réside dans le fait que l'insecte infeste de vastes superficies et qu'il émigre des superficies traitées vers les superficies non traitées. La recherche sur la tordeuse occidentale de l'épinette (*C. occidentalis*), qui infeste des foyers isolés, a été moins intense.

La riposte idéale contre un insecte ravageur serait le lâcher d'un organisme (parasite ou pathogène) qui pourrait se reproduire au milieu de la population à réprimer, s'étendre dans les régions non traitées et réduire les effectifs de l'hôte à un niveau endémique. À défaut d'en trouver une contre la tordeuse, tous les agents actuels de répression sont utilisés de la même façon qu'un pesticide chimique. Ils n'exercent d'effets que sur la génération traitée.

La bactérie *Bacillus thuringiensis* (B.t.) est le seul agent biologique obtenu industriellement et homologué contre la tordeuse. Ces dernières années, son efficacité a beaucoup crû grâce à l'utilisation de préparations très puissantes épandues à faibles doses. Il s'agit maintenant d'une solution viable de rechange aux pesticides chimiques, pour ce qui est de sa rentabilité, et sa vogue s'accroît. Les virus sont coûteux à produire et aucun n'a provoqué d'épizooties majeures; les mycoses ne sont pas encore rendues au point où on peut en faire l'essai par épandage aérien tandis que les protozoaires sont considérés comme peu prometteurs. Le recours à des parasites exotiques n'a donné aucun résultat positif, mais on s'intéresse à des lâchers massifs du parasite des oeufs *Trichogramma minutum*. Seuls des tests préliminaires ont été menés sur les nématodes pathogènes, dont les préparations efficaces restent à trouver pour l'utilisation dans les forêts.

Certains inhibiteurs de la mue se sont révélés très prometteurs suite à des essais sur le terrain et d'ici peu ils pourraient être obtenus industriellement. Le recours aux phéromones sexuelles pour perturber le comportement reproducteur exige encore des recherches et pourrait ne pas supprimer les infestations. La recherche sur les agents antiappétants est encore dans son enfance. On a envisagé des lâchers de mâles stériles, mais on a abandonné cette stratégie.

De nouvelles techniques de manipulations génétiques des micro-organismes sont prometteuses pour ce qui est d'augmenter l'efficacité de B.t. et des virus destinés contre la tordeuse. C'est une brèche dans laquelle on s'engage fébrilement, et il est à souhaiter que des produits nouveaux et améliorés pourront être expérimentés sur le terrain.

Introduction

When the term biorationals was first coined it was used to cover highly specific chemicals which could be used to block biochemical pathways unique to insects — insect growth regulators, and highly specific chemicals which could be used to disrupt mating — sex pheromones. When the Environmental Protection Agency (EPA) in the USA issued a document on data requirements for biorational pesticides, microbial agents were included under this heading and biorational pesticides were defined in the EPA document as "materials such as viruses, bacteria, protozoa, fungi and certain biochemicals, either naturally occurring or synthetically produced, that attract, retard, destroy or otherwise exert a pesticidal activity." As there are currently no registration requirements, and hence no data requirements, for vertebrate or invertebrate predators, parasitic insects or nematodes, these were not included in the EPA definition. The term biorationals is now being used loosely to cover all methods of control, except cultural control, which do not utilize broad spectrum conventional chemical pesticides, and that is how it is used to cover the topics discussed in this review.

The severity of the spruce budworm problem and its economic and social consequences have been ade-

quately covered elsewhere. Until recently, the only operationally feasible method of regulating this insect was the use of chemical pesticides. Although great progress has been made in safe and environmentally acceptable use of the currently registered chemical pesticides, the public is aware of the misuse of chlorinated hydrocarbons in the 1950s and 1960s. To some extent scientists and government officials dealing with pesticides for the control of forest insects have lost their credibility with the public and the situation has been further exacerbated by news media coverage. On the other hand, biological control is sold as a panacea. This is a myth at the present time as biological control techniques are not sufficiently advanced to replace currently used chemical pesticides. There is also a question of cost; a few biological control techniques are very simple to use and inexpensive, but most, when compared to chemical pesticides, are expensive, difficult to apply and slow acting. Pest control should not be a forum for emotion and the public must be educated in the advantages and disadvantages of various pest control strategies. To label conventional chemical pesticides as bad and biological control methods good is an exceedingly naive outlook.

Biorational methods of control can be divided into two broad categories. In the first, materials are used in the same manner as conventional insecticides. They affect only the generation of spruce budworm treated and only insects which encounter a lethal dose. There is no effect on the next generation, no spread from the treated areas and no secondary infection. The advantage of such biorationals compared to broad spectrum chemical pesticides is that they are considered safe, environmentally acceptable, and they usually affect only the target insect, spruce budworm. Beneficial insects such as predators and parasites are unaffected and, when the spruce budworm population is substantially reduced by the initial treatment, it is possible that these natural control factors have a greater impact.

The second category involves self-replicating organisms which, when released into a spruce budworm population, establish themselves and reduce the infestation from an epidemic to an endemic level. Agents having this capability are parasites and some microbial and viral agents. Some agents belong to both categories; an inundative release of a parasite which does not establish in the spruce budworm population and/or alternative hosts has an impact similar to the application of a chemical pesticide. Also viruses and fungi can be applied as insecticides with no hope of long-term establishment and population regulation. Under ideal circumstances small and relatively inexpensive releases of biocontrol agents give long-term regulation of the target insect pest. Unfortunately, records of outstanding successes are limited, and none has been found for the spruce budworm. Most successes have involved introduced pest species that were imported without the array of predators, parasites and diseases which regulate them in their native habitat. In the late 19th century, some glasshouse and citrus pests were successfully controlled by importation of predators and parasites. In the 1930s and 1940s, the European spruce sawfly (*Gilpinia hercyniae*), was as serious a pest on spruce in eastern Canada as the spruce budworm is on the spruce-fir forest today. A combination of a virus and imported parasites terminated this outbreak and reduced European spruce sawfly to an endemic level. It is thought that the virus was accidentally imported from Europe along with parasites which were released for control purposes. With very little human help, the virus and parasites spread throughout the entire range of the host and eliminated a major problem (McGugan and Coppel 1962). A more recent example of the planned release of a virus is the successful program to control the rhinoceros beetle (*Oryctes rhinoceros*), a pest of coconut palms in the South Pacific (Bedford 1981).

There are both positive and negative aspects to using biological agents in a forest situation, compared to using them to control an agricultural pest. On the positive side, the forest environment is longstanding and stable and there is time for a parasite or disease to establish in the insect population. Provided that trees are not killed, or severely damaged and weakened, a certain amount of defoliation and loss of growth increment can be tolerated, although some forest managers may disagree on this point. Hence, slow acting control agents, which would be unacceptable to farmers, are still potentially useful candidates for forestry use. On the negative side, forests cover vast areas, most of which are inaccessible from the ground. The annual per-hectare value of trees is a fraction of that of agricultural crops, thus forest managers are inclined to spend considerably less money than farmers on insect control. Furthermore, it is not feasible to use labor-intensive methods of control in forestry that may be quite attractive in a situation such as an orchard.

Spruce budworm is particularly difficult to control because of the vast area which is infested; defoliation occurred in more than 26.8 million ha (66.2 million acres) in 1983 in eastern Canada and the USA (Kucera and Taylor 1984). Aerial application of most control agents is the only practical method of treatment. Under certain meteorological conditions, adult female budworm moths embark on moth flights and are carried considerable distances by wind currents; shorter local flights also occur and second instar larvae on silk threads can be dispersed by wind currents. Therefore reinvasion of treated areas is always a distinct possibility. Budworm larvae are concealed until budflush, by which time they have reached about the fourth instar, making them more difficult to control than species which feed in an exposed situation during all their larval instars.

Because of the economic importance of the spruce budworm, every possible strategy for regulating it has been evaluated and most have been tested. In this review, an attempt is made to summarize recent research on biorationals for spruce budworm control, evaluate the state-of-the-art, and suggest future avenues of endeavor that may yield promising results. The individual topics covered are parasites and predators, nematodes, microbial control agents which include bacteria, fungi, viruses and protozoa, physiological mechanisms which include insect growth regulators and sex pheromones, antifeedants and genetic mechanisms involving release of sterile males.

Parasites and Predators

Best results with parasites as biocontrol agents have been obtained when they are imported to control exotic species, and only limited successes have been obtained when attempting to control native pests with exotic parasites or when trying to establish a parasite on a new host. Parasite releases on spruce budworm in Canada up until 1980 have been reviewed by Miller and Otvos (1981) and Varty (1984). One limited attempt has been made to establish a predator; red wood ants (*Formica lugubris*) were introduced into a localized area of Quebec. Large numbers of late instar larvae were brought to one nest and there was noticeably less defoliation of trees surrounding that nest (Finnegan 1978).

Between 1944 and 1953, four species, two tachinids, a sarcophigid and an ichneumonid, from unidentified western spruce budworms, were released at various sites from Manitoba to Newfoundland, and between 1948 and 1956, 12 ichneumonid species from European *C. murinana* were released in Ontario and Quebec. None of these releases led to establishment of the parasite (McGugan and Coppel 1962).

In the late 1960s an outbreak of todo pine budworm (*C. diversana*) in Japan yielded more parasite material. An ichneumonid, *Cephaloglypta laricis*, was imported and over a 4-year period, 90,000 spruce budworm larvae were exposed to attack. Oviposition success ranged from 17 to 60 percent, but in rearing thousands of potentially parasitized larvae, only a few adults emerged and only one female oviposited. The most plausible explanation for this failure was that spruce budworm is able to kill and absorb parasite larvae, leaving the host unimpaired. Another ichneumonid, *Lissonota* sp., from *C. diversana* was shipped to New Brunswick in 1972, 1973, and 1975. It appeared to be incompatible with spruce budworm because of low ovipositional stimulus and some innate resistance of the host (Varty 1984).

An ichneumonid, *Cephaloglypta murinanae*, was shipped to New Brunswick from Czechoslovakia in 1972, but the culture disappeared under circumstances similar to the fate of *C. laricis* (Varty 1984). A native sarcophigid fly, *Agria housei*, is a prepupal and pupal parasite of both spruce budworm and western spruce budworm. It can be mass produced on pig liver at low cost, but a laboratory stock reared for many generations lost its cold hardiness and ability to enter diapause (House 1967). In 1971, about 2,800 adult flies, of which 34 percent were female, were released on spruce budworm pupae in New Brunswick. From a sample of 1,114 pupae, collected within 10 days of the release and within 75 m (246 ft) of the release point, 14 *A. housei* puparia were found, but no further specimens were recovered in 1972 or 1973. A chalcid, *Brachymeria intermedia*, is best known as an introduced pupal parasitoid of the gypsy moth. It will also parasitize wax moth and spruce budworm, although gypsy moth is the preferred host (Minot and Leonard 1976). Interest has been expressed in developing *B. intermedia* as a biocontrol agent for spruce budworm in Maine (Leonard 1975).

Parasitoids of the genus *Trichogramma* have been used for biological control of agricultural and orchard pests in the USA for many years (Ridgway et al. 1981), and there is considerable interest in using augmentative releases of *T. minutum* as a strategy for regulation of spruce budworm at the egg stage. Natural parasitism of spruce budworm eggs by *T. minutum* may be as high as 77 percent (Anderson 1976), but typically accounts for 5 to 25 percent and varies greatly by geographical locality and year (Miller 1953, 1963; Neilson 1963; Thomas 1966; Varty 1984). Studies on *T. minutum* were conducted in Quebec between 1970 and 1975 (F.W. Quednau, cited by Varty 1984). Quednau was of the opinion that scarcity of alternate hosts limited the potential of *T. minutum* for exerting a greater impact on the spruce budworm population and he calculated that about 2.5 million female parasitoids/ha would be required for an inundative release. He found a Canadian ecotype, well adapted to the forest environment, which had superior host finding potential; in experiments with caged trees, the maximum levels of parasitism were less than 50 percent. Quednau was frustrated when prohibited from importing angumois grain moth (*Sitotroga cerealella*) into Canada as a host for *T. minutum* production; this species is routinely used as a host for production in the USA.

Field release programs were conducted in Maine in 1977, 1978, 1979, and 1981 (Houseweart et al. 1984a). In 1977, a commercial strain of *T. minutum* was tested at six dosage levels ranging from 31,250 to 2 million parasitoids per 20 m^2 (215 ft^2) plot and parasitism rates of 12.8 percent were recorded compared to 10.4 percent in checks. In 1978, a Maine strain of *T. minutum* was compared to the commercial strain on

20 m^2 plots in three localities with 125,000 parasitoids released at each plot. The Maine strain gave considerably higher levels of parasitism (up to 45.4 percent in one locality) compared to the commercial strain. In 1979, various release strategies were tested using the Maine strain; these were four-point, broadcast, and multiple releases, again on 20 m^2 plots with 125,000 parasitoids per plot. Broadcast was better than multiple release or four-point release, but still not statistically significantly different from the check, and it appeared that there was a problem of parasitoids migrating from these small plots. It was considered that better results would be obtained with an aerial release which would place the *T. minutum* at upper crown levels where spruce budworm egg densities are at their highest (Kemp and Simmons 1978; Jennings and Houseweart 1983a). *S. cerealella* eggs supposedly pick up a static charge when falling through air and will adhere to coniferous foliage following aerial application (M.W. Houseweart, personal communication).

Aerial release trials planned for 1980 were abandoned when three shipments of *S. cerealella* eggs had a parasitization rate of only 5 to 20 percent. In 1981, the Maine strain was applied by helicopter on three 4-ha (10-acre) plots with three releases each, on June 2, 8 and 15 with 410,000, 350,000, and 607,500 female parasitoids applied per ha (166,000, 141,600, and 245,850 per acre). It was considered that the third application may have been too late, due to an early season. On balsam fir trees 5.1 percent of eggs were parasitized on the treated area and 2 percent on the check, but on spruce trees there was no difference from the checks. It was planned originally to apply 3.75 million females/ha (1.5 million/acre) and the 1.37 million (553,500) applied may have been too low to regulate an epidemic spruce budworm population.

T. minutum releases were conducted in northern Ontario in 1982 and 1983 with both ground and aerial application of parasitized eggs. In 1982, it was originally planned to have three releases, 5 to 7 days apart, but insufficient material was available. Treatment of a 1.25-ha (3-acre) plot at 250,000 females/ha (101,000/acre) gave negligible levels of parasitism compared to untreated checks. In 1983, one release was made during the middle of the oviposition period and a 2-ha (5-acre) plot was sprayed with 6.5 million females/ha (2.63 million/acre). An Ontario strain of the parasitoid, reared in California and shipped to the application site, was used. In the release area, levels of egg parasitism ranged from 22 to 62 percent compared to very low to negligible levels recorded outside the release area (S.A. Nicholson, personal communication). These results are considered to be most encouraging in the treatment of an epidemic population.

Several important basic biological studies have been conducted in Maine on the relationship between *T. minutum* and spruce budworm in the forest ecosystem. A comparison of the parasitoid reared in *S. cerealella* eggs and *C. fumiferana* eggs showed faster development in the former. Further studies are required to determine the effect of different hosts on nutrition, vigor and fecundity of parasites to be used for field releases (Lawrence et al. 1985). Oviposition of female *T. minutum* was over a longer period in *S. cerealella* eggs than in *C. fumiferana* eggs (Houseweart et al., 1983) and female *T. minutum* from *C. fumiferana* eggs were considerably larger than those from *S.cerealella* eggs (Southward et al. 1982). *T. minutum* does not overwinter in *C. fumiferana* eggs (Jennings and Houseweart 1983a). Spruce budworm egg deposition took place over a 27-day period both in 1979 and 1980 and it was found that parasitism rates were greater in 1- to 3-day old than in 6- to 8-day old eggs (Houseweart et al., 1982).

To obtain high levels of natural parasitism with *T. minutum*, alternate hosts to spruce budworm are essential; greenstriped mapleworm, birch casebearer, saddled prominent, and forest tent caterpillar have been identified as alternate hosts in mixed stands of deciduous and coniferous trees, although eggs of several other species are probably parasitized (Houseweart et al., 1984b). In Maine, it is believed that multiple broadcast aerial releases are feasible for suppression of endemic, but not epidemic, spruce budworm populations and this technique is particularly attractive in environmentally sensitive areas (Houseweart et al. 1984a). In Ontario, it is not anticipated that periodic releases of *T. minutum* will augment naturally occurring levels of parasitism and maintain spruce budworm populations below an economic threshold. However, releases that inundate special areas, such as high value stands, plantations, and seed orchards may prove to be another possible control option in a situation where there are few alternatives to chemical pesticides (S.A. Nicholson, personal communication).

There is considerable interest in rearing *Trichogramma* spp. on artificial media as a substitute for insect eggs. *T. minutum* has not been reared *in vitro*, but this has been accomplished with *T. pretiosum* in the USA (Hoffman et al. 1975) and *T. dendrolimi* in China (Guan et al. 1978; Wu et al.1980). Mass production of adult *Trichogramma* has yet to be achieved on artificial media, but, if successful, will drastically reduce the production costs of these egg parasites.

Nematodes

Nematodes are round worms that parasitize almost every kind of animal and plant in the world. They have been found in many species of insects and a few have been developed successfully as biocontrol agents. Nematode-insect interactions can range from phoresy to obligate endoparasitism and include death of the host, sterility, reduced fecundity, delayed development, and aberrant behavior. In some cases, bacteria associated with the nematodes are the actual cause of death of the insects. The use of nematodes for spruce budworm population regulation has been considered and tests have been conducted on both the eastern and western species. Nematodes can be propagated *in vivo* in such hosts as the greater wax moth (*Galleria mellonella*), or *in vitro* on such substrates as dog food or waste meat products.

In laboratory tests, it was found that both larvae and pupae of spruce budworm were susceptible to a neoaplectanid nematode, *Neoaplectana carpocapsae* (Schmiege 1963). A rhabditid nematode, *Heterorhabditis heliothidis*, was tested in the laboratory on fourth, fifth and sixth instar larvae and on pupae (Finney et al. 1982). At 24°C (75°F), 120 nematodes/larva gave 100 percent mortality in 48 h, but at 17°C (62°F) this took 120 h; at 24°C, 80 percent and 73 percent mortalities were recorded for pupae exposed to 150 and 60 nematodes/pupa, respectively. Further tests were undertaken on first, second and third instar larvae (J.R. Finney and G.F. Bennett, personal communication). It is possible to infect these stages under laboratory conditions. However, cycling of the nematode, which would result in secondary infection, cannot occur in first instar larvae as host cadavers disintegrate before the process is completed. After measuring webbing on hibernacula of second instar larvae and the diameter of the nematodes, it was concluded that it is unlikely that they can penetrate this webbing. Therefore, this nematode would be ineffective against first and second instar larvae under field conditions.

The effect of *N. carpocapsae* and its mutually associated bacterium, *Xenorhabdus nematophilus*, has been tested on western spruce budworm in laboratory and small-scale field trials (Kaya et al. 1981). In the laboratory, mortality of fourth instar larvae was 100 percent 72 h after application of 1000 and 4000 nematodes/mL in 2 percent aqueous Volck oil. In another test, fourth and fifth instar larvae were placed on Douglas-fir seedlings. On uncovered seedlings treated with 1000 and 4000 nematodes/mL, mortality was less than 25 percent, again on uncovered seedlings 4000 and 8000 nematodes/mL gave 26 and 59 percent mortality, but when covered with plastic bags to maintain a high humidity, 4000 and 8000 nematodes/mL gave 60 and 91 percent mortality, respectively. There was no significant population reduction following field trials in three localities in which 2-3 m (6.5-10 ft) naturally-infested grand fir were sprayed to run off with 4000 and 8000 nematodes/mL. Air temperature at the time of application did not exceed 15°C (59°F) and rain fell after all applications; these factors may have adversely affected the results.

In another field trial, Kaya and Reardon (1982) tested four tank mixes containing various antidesiccants. These tank mixes had previously been tested with *N. carpocapsae* on Colorado potato beetle (MacVean et al. 1982). Fourth and fifth instar western spruce budworm larvae on 2-3 m (6.5-10 ft) grand fir trees were sprayed with formulations containing 16,000 nematodes/mL and each tree received from 8×10^6 to 1.3×10^7 nematodes. Applications were made at night when low temperatures and high humidity favored nematode survival, but reduced infectivity. In spite of the antidesiccants, significant infections of larvae and pupae were not obtained.

The most successful use of *N. carpocapsae* has been in moist environments such as the soil or in galleries of boring insects (Gaugler 1981). It is felt that use of this nematode against feeding spruce budworm larvae is not a worthwhile endeavor unless some effective method is found for protecting nematodes from desiccation when they are applied as foliar sprays (H.K. Kaya, personal communication).

Bacillus thuringiensis

Bacillus thuringiensis (B.t) is a bacterium of the genus *Bacillus* that is pathogenic to insect larvae, mainly in the order Lepidoptera. In common with other bacteria in this genus, it is a rod-shaped spore former and is motile with peritrichous flagella. When it sporulates, B.t. forms a protein parasporal body called the delta-endotoxin, which is often referred to as the crystal. When sporulation is complete, the bacterial cell lyses and both the spore and crystal are released into the surrounding medium.

Bacillus sotto was isolated from silkworm in 1901 by Ishiwata and in 1911, Berliner isolated a bacterium from Mediterranean flour moths which he named *B. thuringiensis*. It was later determined that *B. sotto* and *B. thuringiensis* were strains of the same species (Fast 1974; Dubois and Lewis 1980). Metalnikov and Chorine (1929) reported on gypsy moth control with B.t., but it was not until the early 1950s that serious commercial production was begun (Hall 1963) and most applications were on agricultural pests. Until the early 1960s, formulations of B.t. were prepared from the Berliner strain and in the late 1960s an improved strain, HD1, was adopted for commercial production (Dulmage 1970).

The relative roles of spores and crystals in B.t. preparations fed to spruce budworm has frequently been a topic for debate. Clean preparations of crystals are 200 times more lethal than clean preparations of spores when compared on a weight basis (Fast 1977), although mixtures of spores and crystals are slightly more toxic than crystals alone. The crystals are toxic only after being ingested by larvae and activated by proteolysis, and they act by destroying the gut epithelium (Percy and Fast 1983). The action of B.t. in spruce budworm is cumulative; if larvae have access to clean food before a lethal dose is ingested they may recover and pupate normally. Feeding inhibition occurs soon after ingestion of B.t., but larval death does not occur until hours, or in many cases, days after exposure (Fast and Régnière 1984). Feeding reduction due to inhibition may result in less foliage damage even though larval survival may be greater than desired.

The crystal is pure protein and is composed of dimeric subunits with molecular weights of 230,000 daltons. The monomer has a molecular weight of 130,000 daltons determined by electrophoresis. When the monomer is hydrolyzed in the larval gut, peptides of 60,000 daltons each are produced and these are the active toxins (Fast 1985). Evidence that the gene for the toxin is on a plasmid has stimulated a great deal of interest in engineering improved forms of the crystal.

The delta-endotoxin gene has been cloned in *E. coli* (Schnepf and Whiteley 1981) and in *B. subtilis* (Klier et al. 1982). Part of the DNA sequence of the delta-endotoxin gene has been determined (Wong et al. 1983). Genetic manipulation may lead to the development of strains with increased toxin yields or enhanced specific activity, to hybrid delta-endotoxins with altered host spectra or to the production of this metabolite by vegetative cells (Luthy et al. 1984).

There is considerable interest in determining the interaction of spruce budworm larvae and a foliar spray application of B.t. and developing a B.t. – spruce budworm model. What is the optimal droplet size? What dosage of B.t. should be in that droplet? How long does the B.t. remain toxic on the foliage? How much foliage do spruce budworm larvae ingest? Using an amaranth dye and spectroscopic analysis of faeces, the food intake of fourth, fifth, and sixth instar spruce budworm larvae over a 24-h period has been determined (Retnakaran 1983). Results indicated that the sixth instar consumed 20 times more than fourth instars and fifth instars consumed three times more than fourth instars. Fourth instar larvae consume an average 14.4 mm^2 (0.02 in^2) balsam fir foliage daily (Fast 1981).

When field dosages were compared to "one-shot" laboratory dosages, it became obvious that mortality in the field is much higher than one would predict from laboratory experimentation and it became clear that the length of time of exposure in the field was a critical factor as well as the dosage (Fast and Régnière 1984). There is the possibility of recovery of larvae which ingest a sublethal dosage of B.t. and data suggest that, in the field, larvae may repeatedly recover from feeding inhibition and reinfect themselves if active B.t. is still available. Extension of the exposure period from 1 day to 6 days resulted in a 500-fold reduction in the LC_{50}, i.e., a 500-fold increase in susceptibility, and a reduction in the length of time to death as well. Fast and Régnière concluded that factors affecting B.t. as a control agent are spray deposition and distribution on the foliage, B.t. degradation due to weathering, larval feeding and development rates, and cycles of feeding inhibition and recovery, all of which can be affected by temperature, relative humidity, and precipitation. These are essentially the same conclusions reached by Walton and Lewis (1982) following analysis of results of field trials.

Using diet incorporation assays, no differences in susceptibility were found between fourth, fifth, and sixth instar larvae exposed to B.t. in terms of LC_{50} and LT_{50} (Fast and Dimond 1984). They also sprayed small plots of 2.5 m (8 ft) tall balsam fir tees with a mistblower applying dosages of 5.5. 10.9 and 21.9 Billion International Units (BIU)/ha (2.2, 4.4, 8.8 BIU/acre) when larvae were peak of the third instar, early fourth instar, peak of the fourth, peak of the fifth, and peak of the sixth instar. Most effective control was obtained at fourth and fifth instars. Poor control of sixth instar was attributed to a significant proportion having reached the nonfeeding prepupal stage at the time of application. It is suggested that the period during which B.t. can be applied can be extended to include populations which are at the peak of the fifth instar. Traditionally, peak of the fourth instar has been regarded as the optimal timing for B.t. applications, and this extension could allow spray operators a little more latitude.

Considerably more research is required to complete this model and verify it in the field. Progress towards determining the required number of droplets/needle has been made using a balsam fir model in the laboratory (P.G. Fast and A. Sundaram, personal communication) and in the field (P.G. Fast, E. Kettella, and C. Wiesner, personal communication), but no data are available on spruce hosts. The impact of B.t. on spruce budworm on balsam fir begins to show an effect when a 6.3 BIU/L preparation is sprayed at 0.5 droplets/needle at a dosage of 30 BIU/ha (12 BIU/acre) in 4.7 L/ha (½ gal/acre), and it is probable that optimal results are obtained with 2 to 3 droplets/needle at this concentration. Higher concentrations are expected to be efficacious at lower deposit densities.

The current trend toward using undiluted, neat formulations has major benefits in reducing application costs and eliminating mixing, with its attendant equipment and pitfalls, as well as providing easier calibration of spray equipment and reducing the risk of contamination. Much of the recent improvement in efficacy and reliability can be attributed to the use of more concentrated preparations because each droplet carries a higher load of toxicant (P.G. Fast, personal communication). A 6-fold increase in concentration from 2.1 to 12.6 BIU/L is sufficient to increase mortality by more than 50 percent at a given droplet size and deposit density. The use of more concentrated formulations has also permitted reduction of emitted volumes from 9.4 L/ha (1 gal/acre) to 2.4 L/ha (¼ gal/acre) or even 1.75 L/ha (3⁄16 gal/acre) while maintaining the same dosage.

Three companies in North America presently manufacture B.t. products labelled for spruce budworm control. They are Abbott Laboratories, Zoecon Corporation (Subsidiary of Sandoz, Ltd.) and Biochem Products (Division of Salsbury Laboratories). About 12 formulations are registered for forestry use. The trend in recent years has been to produce more concentrated formulations which can be applied undiluted. Abbott's oil-based Dipel® 6L (called 132 in Canada) contains 12.7 BIU/L and a new oil-based formulation Dipel® 8L (176) contains 16.8 BIU/L. Abbott is presently testing a new water-based formulation. Zoecon's Thuricide® 48LV contains 12.7 BIU/L and Biochem's Futura® contains 14.5 BIU/L. Two new Biochem products, one oil-based and one water-based, containing 13.2 BIU/L, are being developed. These liquid formulations are a major improvement on the wettable powders that were first used for spruce budworm control, but still there are problems with both oil- and water-based formulations. There are no oil-soluble stickers if oil formulations are used undiluted and oils can cause damage to automobile paint. Water formulations have a high evaporation rate and can cause problems in delivery systems (F.B. Lewis, personal communication).

The first field trials with B.t. during the 1960s gave variable results (Mott et al. 1961; Klein and Lewis 1966). The commercial availability of the HD1 strain renewed interest in field testing (Tripp 1972; Smirnoff et al. 1972) and early trials have been reviewed by Harper (1974), Morris et al. (1975), and Morris (1982a). During the 1970s, there was interest in the addition of the enzyme chitinase to B.t. preparations. Smirnoff suggested that the addition of this enzyme increases the permeability of the larval gut and facilitates penetration of spores into the hemocoel (Smirnoff 1971, 1973, 1974a). Aerial applications of B.t. mixed with small amounts of chitinase have given conflicting results (Dimond 1972; Smirnoff 1974b; Dimond 1974; Morris 1976). Because of problems of registration of material containing an enzyme, further research on this aspect was terminated.

More recently, Morris has conducted extensive field trials with registered products to determine the optimum dosage, emitted volume and number of spray applications required for acceptable control and foliage protection with B.t. In 1981, he tested dosages of 10, 20, 40, and 80 BIU/ha (4, 8, 16, and 32 BIU/acre) of both Thuricide® 32BX and Dipel® 88 in 9.4 L/ha (1 gal/acre) on 20-ha (50-acre) plots. He found the dosage of 20 BIU/ha (8 BIU/acre) was only marginally effective against a population of 12 to 36 larvae/45 cm branch tip and advocated a dosage of 30 BIU/ha (12 BIU/acre). In 1982, he tested Thuricide® 48B at 30 BIU/ha (12 BIU/acre) in emitted volumes of 2.4, 4.7, and 9.4 L/ha (¼, ½, and 1 gal/acre) and Dipel® 48B at 30 BIU/ha (12 BIU/acre) in 2.4 L/ha (¼ gal/acre) on 20-ha (50-acre plots). He concluded that a volume of 2.4 to 4.7 L of spray/ha was more effective than higher volumes (Morris 1984a). In tests comparing double versus single applications of B.t., Morris found that double applications of half the dosage are not significantly more effective than single applications of the full dosage (Morris 1984b). He used Dipel® 88 at 2 × 10 BIU/ha (4 BIU/acre) and 1 × 20 BIU/ha (8 BIU/acre) and Thuricide® 32B at 2 × 20 BIU/ha (8 BIU/acre) and 1 × 40 BIU/ha (16 BIU/acre).

Dimond (1982) obtained excellent results with undiluted formulations of 32B and 48B applied at 30 BIU/ha (12 BIU/acre) on 162-ha (400-acre) blocks in emitted volumes of 3.2 and 2.4 L/ha (⅓ and ¼ gal/acre). Over a period of several years, Smirnoff developed a B.t. product that he called Futura, which is based on a sorbitol formulation. In 1983, Futura was registered by Biochem and is commercially available. Futura® was field tested in 1981, 1982, and 1983 (Smirnoff et al. 1982; Smirnoff and Valero 1983). Smirnoff has obtained consistently good results applying Futura® at 20 BIU/ha (8 BIU/acre) in 2.5 L/ha (¼ gal/acre) using small aircraft on small blocks and four-engine aircraft on large areas. Deposits of 80 percent emitted volume have been recorded, larval mortality was in the range of 70-90 percent and about 70 percent of the foliage has been protected (Smirnoff 1985).

Following inconsistent results reported from B.t. applications, it was decided to apply and evaluate two B.t. formulations, Thuricide® 16B and Dipel® 4L, in four different geographical localities in 1980; Maine, New Hampshire, Wisconsin and Arizona. Western spruce budworm was the target in the Arizona application and this part of the trial is discussed later. Each treatment was replicated five times on 20-40-ha (50-100-acre) blocks in each locality with a dosage of 20 BIU/ha (8 BIU/acre) in an emitted volume of 9.4 L/ha (1 gal/acre) (Walton and Lewis 1982). Severe problems with weather and operational delays were encountered in all localities except Wisconsin where the application was made as specified when 80 percent of the larvae were in the third and fourth instars. In Wisconsin, the 20 BIU/ha (8 BIU/acre) dosage gave high population reductions (Reardon et al. 1982). Walton and Lewis (1982) concluded that the apparent sensitivity to weather and timing of applications remain serious impediments to B.t. acceptance and suggested that this sensitivity may be reduced by using dosages higher than 20 BIU/ha (8 BIU/acre), improving the formulation, and applying multiple treatments.

Multi-year benefits and carry-over effects following B.t. treatments have been discussed in some reports. Morris (1977) recorded less defoliation and low oviposition rates in B.t.-treated plots compared to untreated areas over a period of 2 to 3 years. Dimond and Spies (1981) noted that there was much less defoliation in B.t.-treated plots than in untreated areas in the year after the application. It has been suggested that "metabolic perturbations" in survivors of B.t. treatments affect fecundity and population density the following year (Smirnoff et al. 1974). However, Dimond considers that this phenomenon is due to lack of re-invasion of treated plots and is not due to any carry-over effect (J.B. Dimond, personal communication).

Morris (1975) screened a variety of B.t.-chemical insecticide combinations against spruce budworm and found acephate (Orthene®) was a promising candidate. Aerial applications in Ontario of 20 BIU/ha (8 BIU/acre) Dipel® WP plus 42 g (1.5 oz) of Orthene® in 2.35 to 4.7 L/ha (¼ to ½ gal/acre) gave 17-34 percent higher spruce budworm mortality than Dipel® alone (Morris and Armstrong 1975; Morris 1977). Orthene® alone applied at 420 g/ha (6 oz/acre) caused no spruce budworm mortality the same year in nearby plots (Armstrong and Nigam 1975). The B.t.-Orthene® treatment provided some foliage protection in the year of application and the spruce budworm population remained low for a period of 3 years. In another test in Ontario, 20 BIU/ha (8 BIU/acre) Dipel® 36B and Thuricide® 16B plus 56 g (2 oz) Orthene® in 9.4 L/ha (1 gal/acre) provided excellent larval mortality and foliage protection in the year of application (Morris et al. 1979).

Results in Maine have been less satisfactory. Inconclusive results were obtained with B.t.-Orthene® combinations with far greater dosages of Orthene® than recommended by Morris (Dimond 1975). Further tests were conducted in Maine in 1979; 20 BIU/ha (8 BIU/acre) Thuricide® 16B plus 56 g (2 oz) Orthene® did appear slightly more effective than the same dosage of B.t. alone, but not statistically so, and plots treated with the combination received the lowest mean spray deposit (Dimond and Spies 1980). This line of research has not been pursued further; the addition of a chemical insecticide defeats some of the benefits of using B.t.

Presently over 1100 strains of B.t. have been isolated from worldwide sources. In Canada, 50 isolates were bioassayed and none was more potent to spruce budworm than the HD1 strain presently used in commercial preparations (Morris and Moore 1983). In the USA, 298 strains have been screened against spruce budworm and 350 against gypsy moth (N.R. Dubois, personal communication). Of these about 5 percent were better against these two major forest insect pests than commercially produced HD1, with four strains very potent and worthy of further investigation. While conducting these assays, Dubois found a new strain of B.t. in spruce budworm shipped from Canada. Against spruce budworm, the LC_{50} of this strain is half that of HD1 and the LT_{50} is also half. This new strain is also highly effective against gypsy moth and several major agricultural pests. It has the same potency as HD1 against cabbage looper which is a standard test insect for B.t.

Sandoz Ltd. prepared a batch of the new strain, SAN 415 32LV, which was compared to Thuricide® 32LV in 1983 when two plots in Maine, 121 ha (300 acres) and 202 ha (500 acres), were treated with these products. There was no significant difference in larval mortality, but the new strain gave greater foliage protection, probably because it is faster acting (N.R. Dubois, K.D. Murray and J.B. Dimond, personal communication). Further field trials with this new strain are planned in Maine, Quebec, and New Brunswick in 1984 and it is also intended to test it on western spruce budworm.

Considerably less research has been conducted on the western spruce budworm than on the eastern species. In the USA, the first trial in Montana was conducted using Dipel® wettable powder (McGregor et al. 1976). Thompson et al. (1977) compared three application rates, two spray droplet spectra, and five formulations in Washington. The most effective formulation contained 25 percent sorbitol and 50 g/L Shade® sunscreen applied in coarse droplets (vmd 300 μm). Generally, these trials have shown unacceptable control of larval population, but moderate foliage protection. In 1978, four 40-ha (100-acre) plots in British Columbia were treated with Thuricide® 16B at 20 BIU/ha (8 BIU/acre) and 15 days postspray population reductions due to treatment were 32, 66, 79, and 91 percent (Hodgkinson et al. 1979). Populations were monitored for the next 2 years and increased dramatically in 1980 (Shepherd et al. 1982).

In 1980, the effectiveness of Thuricide® 16B, Thuricide® 32B and Dipel® 4L were compared in Arizona as part of the program conducted in four geographical localities including Maine, New Hampshire, and Wisconsin. These applications on the eastern species have already been discussed. The dosage was 20 BIU/ha (8 BIU/acre) in an emitted volume of 9.4 L/ha (1 gal/acre) and each of the three treatments was applied to five replicated 32.4-ha (80-acre) plots. At the time of application 80 percent of the larvae had reached the fifth instar. At 26 days postspray, budworm mortality averaged about 90 percent on the treated plots, but reached 80 percent on the untreated check plots, mainly due to starvation. Bioassays showed that more than 50 percent of the original activity of B.t. spray deposits was lost within 3 days and 97.8 percent within 5 days of spraying. Foliage protection was poor because of the delay in treatment (M.J. Stelzer and D.M. Scott, personal communication).

In 1979, a ground spray application of B.t. in Montana gave excellent results (M.J. Stelzer, personal communication). A truck-mounted hydraulic sprayer was used to apply materials at the peak of the fourth instar to Douglas-fir and Engelmann spruce up to 16 m (52 ft) tall. Effective control and excellent foliage protection were obtained using a tank mix containing 16 BIU/375 L (99 gal) of spray with 5 percent (v/v) molasses added. Double this dosage did not significantly improve results.

In 1981, in New Mexico, nine blocks averaging 600 ha (1483 acres) were selected; three were treated with Dipel® 4L, three with Thuricide® 16B and three served as checks. B.t. was applied at a dosage of 20 BIU/ha (8 BIU/acre) in a volume of 9.4 L/ha (1 gal/acre) when 50 percent of the larvae were in the fourth, fifth, and sixth instars. At 21 days postspray, the average, unadjusted larval mortality was 79.8 percent in the Dipel® 4L blocks, 88 percent in the Thuricide® 16B blocks, and 59.7 percent in the checks. There was no foliage protection in the year of treatment. However, in 1982 defoliation estimates in the Dipel® 4L blocks averaged 16.1 percent, in the Thuricide® 16B blocks 5.6 percent, and in the checks 66.4 percent. This study is being continued (Ragenovitch 1983).

Under the auspices of the CANUSA Program, attempts were made to evaluate the overall operational spray program with B.t. in eastern Canada and Maine, and to compare effectiveness in terms of population reduction and foliage protection and to relate these factors to dosage, deposit, and cost. The area of spruce-fir stands treated in 1979 totalled 44 499 ha (109,956 acres), 100 413 ha (248,120 acres) in 1980 and 79 348 ha (196,069 acres) in 1981 including 365 ha (902 acres) in Manitoba (Morris 1980, 1981, 1982b). Successful applications were defined as those that limited defoliation to 50 percent or less of current year's foliage.

In 1979, registered commercial products Thuricide® 16B and Dipel® 4L were applied along with several experimental formulations such as Thuricide® 24BA, BC and 32B, Novabac® 3 and 45B, and Dipel® AGB 6103 and 45B. Of 28 treatments on balsam fir and white spruce, 15 stands, or 55 percent, met the 50 percent maximum defoliation standard and 6 of 7 treatments, or 85 percent, on red spruce were successful. When overall success was calculated on the basis of total treated area protected, figures were higher with 69 percent for balsam fir and 91 percent for white spruce.

In 1980, based on the proportions of treated areas successfully protected, the figures were 67 percent on white spruce, 99 percent on red/black spruce, and 71 percent on balsam fir. Products applied were Thuricide® 16B, 24B and 32B, Dipel® 88, and Novobac® 3. In 1981, overall success rates of registered B.t. products ranged from 88 to 100 percent. In red, white and black spruce stands, success rates ranged from 85 to 100 percent, but population densities were generally low on spruce. The overall success rate on the more vulnerable balsam fir stands with moderate-to-high population densities was 88 percent, representing a marked improvement over treatments in 1979 and 1980. The following products were used in 1981: Thuricide® 16B and 32B, Dipel® 88 (4L), and to a limited extent, experimental formulations Thuricide® 32BX, Thuricide® 24B, and Futura® 64B. Analysis of the 1981 data indicated that an operational dosage rate of 20 BIU/ha (8 BIU/acre) produces inconsistent results in terms of effectiveness but 30 BIU/ha (12 BIU/acre) is consistently effective and only slightly less effective than conventional chemical pesticides.

Areas in eastern Canada treated with chemical insecticides and B.t. between 1979 and 1983 in eastern Canada and Maine are given in Table 1 and projections for control operations in 1984 are given in Table 2. After a meeting organized by the New Brunswick Dept. of Natural Resources in Fredericton, an overview of the current situation regarding the operational use of B.t. was prepared by Carrow (1983) who summarized data presented by representatives of four provinces and the state of Maine under the headings of cost, effectiveness for foliage protection, operational considerations, and environmental constraints.

The cost of B.t. products declined significantly between 1980 and 1983 with the average cost per BIU dropping from 68 cents to 32 cents. Costs per hectare fell from $6.96 (Can.) to $3.18 (Can.) between 1980 and 1983 in spite of a general increase in dosage from 20 BIU/ha (8 BIU/acre) to 30 BIU/ha (12 BIU/acre). During this period application costs of all pesticides have steadily increased with the result that total costs of B.t. applications have remained constant at about $27/ha. B.t. applications have always been more costly than chemical insecticides, but the differential is diminishing with the increasing cost of chemicals. Currently, B.t. application costs are 1.5 times higher than chemicals in Ontario and Maine and 2.5 to 3.0 times higher in New Brunswick and Quebec.

The effectiveness of B.t. products was considered inconsistent, but in 1983 there was agreement among users that, particularly when used at 30 BIU/ha (12 BIU/acre), foliage protection was as good as that obtained with chemical insecticides. Several factors have probably contributed to this improvement and include more concentrated B.t. products, better application technology, and the use of higher dosages.

Variability in product potency can be a problem (Beegle 1985), but usually potency exceeds that stated on the label. Many products used to require dilution with water and deteriorated if diluted and not applied. However, the development of highly concentrated

Table 1
Area of operational spraying against spruce budworm in Eastern Canada and Maine, 1979-1983

Provinces or state	Year	Total		B.t.		Chemical		% B.t.
		(ha)	(acres)	(ha)	(acres)	(ha)	(acres)	
Ontario	1979	20 250	50,038	3 454	8,535	16 796	41,503	17
	1980	9 948	24,582	4 374	10,808	5 574	13,773	44
	1981	9 801	24,218	6 576	16,249	3 225	7,969	67
	1982	3 429	8,473	3 068	7,581	361	892	90
	1983	3 162	7,813	2 763	6,827	399	986	87
Quebec	1979	582 965	1,440,506	17 030	42,081	565 935	1,398,425	3
	1980	188 511	465,811	22 180	54,807	166 331	411,004	12
	1981	705 164	1,742,460	15 001	37,067	690 163	1,705,393	2
	1982	1 298 557	3,208,734	31 877	78,768	1 266 680	3,129,966	2
	1983	1 253 605	3,097,658	45 627	112,744	1 207 978	2,984,914	4
New Brunswick	1979	1 601 000	3,956,071	205	506	1 600 795	3,955,564	1
	1980	1 614 000	3,988,194	10 500	25,945	1 603 500	3,962,249	0
	1981	1 900 000	4,694,900	0	0	1 900 000	4,694,900	0
	1982	1 693 000	4,183,403	4 000	9,884	1 689 000	4,173,519	1
	1983	1 494 000	3,691,674	10 300	25,451	1 483 700	3,666,223	1
Nova Scotia	1979	556	1,374	556	1,354	0	0	100
	1980	25 670	63,431	25 670	63,431	0	0	100
	1981	31 194	77,080	31 194	77,080	0	0	100
	1982	19 153	47,327	19 153	47,327	0	0	100
	1983	20 726	51,214	20 726	51,214	0	0	100
Newfoundland	1979	5 870	14,505	5 870	14,505	0	0	100
	1980	11 761	29,061	11 761	29,061	0	0	100
	1981	239 983	592,998	1 900	4,695	238 083	588,303	1
	1982	47 843	118,220	4 725	11,675	43 118	106,445	10
	1983	73 380	181,322	0	0	73 380	181,322	0
Maine	1979	1 109 717	2,742,111	16 600	41,019	1 093 117	2,701,092	2
	1980	491 093	1,213,491	80 972	200,082	410 121	1,013,409	17
	1981	474 773	1,173,164	51 203	126,523	423 570	1,046,641	11
	1982	332 006	820,387	36 238	89,544	295 768	730,843	11
	1983	343 981	849,977	66 519	164,368	277 462	685,609	19

Table 2
Proposed area to be sprayed for spruce budworm control in Eastern Canada and Maine in 1984

Province or state	Total		B.t.		Chemical		% B.t.
	(ha)	(acres)	(ha)	(acres)	(ha)	(acres)	
Ontario	4 400	10,872	4 000	9,884	400	988	91
Quebec	800 000	1,976,800	300 000	741,300	500 000	1,235,500	38
New Brunswick	1 000 000	2,471,000	30 000	74,130	970 000	2,396,870	3
Nova Scotia	26 000	64,246	26 000	64,246	0	0	100
Newfoundland	26 000	64,246	3 000	7,413	23 000	56,833	12
Maine	300 000	741,300	100 000	247,100	200 000	494,200	33

formulations, which can be applied neat, has overcome this problem and has reduced the costs associated with high volume applications. Viscosities of different formulations vary and accurate calibration of aircraft is essential. The timing of B.t. applications is more critical than for chemical insecticides as larvae must be exposed and actively feeding.

Carrow criticised inconsistencies of Provincial (State) regulatory authorities in imposing setback zones for human habitation, municipal water supplies, open water, and cultivated land. Every jurisdiction surveyed had different requirements ranging from Maine which had none, to Quebec which had a 1 km setback. Carrow felt that the safety of B.t. had been adequately proved and there should be no setbacks for B.t. applications. He also pointed out that excessive setbacks prevent protection of significant areas of productive forest.

Fungi

Throughout the range of *Choristoneura* spp. in North America, fungi represented by the genera *Erynia*, *Entomophaga*, and *Conidiobolus* (Entomophthorales), and *Metarhizium*, *Beauveria*, *Hirsutella*, and *Paecilomyces* (Fungi Imperfecti) are commonly occurring natural pathogens (Tyrrell 1981; D.F. Perry, personal communication). The most frequently encountered are *Entomophaga aulicae* (=*Entomophthora egressa*) and *Erynia radicans* (=*Zoophthora radicans* = *Entomophthora spaerospe.ma*). In Maine, Newfoundland, and Ontario, percentage mortality due to Entomophthorales fungi has been reported to be as high as 45 percent (Vandenberg and Soper 1975), 60 percent (Otvos and Moody 1978), and 60 percent (D.F. Perry, personal communication), respectively. In Maine, *E. aulicae* and *Conidiobolus* sp. were involved, *E. aulicae* was dominant in Newfoundland, and in Ontario, *E. radicans* was dominant in epizootics observed in 1974 and 1979 (Harvey and Burke 1974; D. Tyrrell, personal communication) and *E. aulicae* in an epizootic observed in 1981 (D. Tyrrell, personal communication). In the majority of infections reported in the literature, death occurred when larvae were in the fifth or sixth instars. However, *Paecilomyces*-killed overwintering second instar larvae have also been observed (D.F. Perry, personal communication). Epizootics of the magnitude caused by Entomophthorales have not been observed with imperfect fungi although the presence of *Beauveria* and *Paecilomyces* at enzootic levels is widespread.

Any naturally occurring fungal pathogens may be potentially useful agents for regulating spruce budworm populations. Entomophthorales would be the fungal agent of choice to initiate and maintain an epizootic, but development of the epizootic would be slow and little foliage protection would be achieved following an application. On the other hand, imperfect fungi could be applied as a biological insecticide in the same manner as B.t. treatments. The treatment would be fast acting and foliage protection could probably be achieved. Unlike viruses, bacteria, and protozoa, which need to be ingested to cause infection, fungi infect insects by penetrating the cuticle.

Because of the spectacular epizootics which have been observed, interest was first focused on the Entomophthorales. Three propagules, hyphal bodies, conidia, or resting spores can be used to disseminate them. Hyphal bodies are very susceptible to biodegradation and conidia are not very stable. Resting spores are the first choice for development as a biocontrol product. Major problems have been encountered in attempting to mass produce resting spores in culture, but they can be produced *in vivo* by injecting insect larvae. Attempts to propagate *E. aulicae in vitro* led to the discovery of a protoplast stage, and this was the first fungus to be grown in a wall-less form (Tyrrell and MacLeod 1972). Subsequent studies have shown that the protoplast stage is part of the natural life-cycle of this fungus and other Entomophthorales. Protoplasts of *E. aulicae* can be cultured *in vitro* and have been studied in detail (Dunphy and Nolan 1977, 1979; Dunphy et al. 1978).

Resting spores of *Erynia radicans* have been produced *in vitro*, although yields have been poor in liquid culture (D. Perry, personal communication). Germination of resting spores has been extensively studied (Perry et al. 1982a; Perry and Whitfield 1984). Storage at 4°C (39°F) and 100 percent RH for 4 to 5 months is required to break dormancy. Resting spores have traditionally been favored for application due to their comparatively high environmental persistence, but they are slow to germinate and this factor must be considered in the timing and type of application (Perry et al. 1982b). The persistence of conidia in the environment is higher than previously thought, in part due to secondary sporulation (D.F. Perry, personal communication). The factors which influence conidial germination have been reported by van Roermund et al. (1984). The optimum temperature for resting spore germination is 12°C (54°F) and for conidial germination, 25-28°C (77-82°F).

To date, field trials with fungi on spruce budworm have been few and on a small scale. In 1981 and 1982, *E. aulicae* and *E. radicans* were released on small trees artificially infested with budworm larvae. Parallel studies were conducted in Ontario and Newfoundland. In 1982, using *E. aulicae* conidia produced *in vivo* and *E. radicans* conidia produced *in vitro*, it was possible to cause mortality greater than 60 percent in populations composed of fourth, fifth and sixth instar larvae (K.P. Lim and D.F. Perry, personal communication). In 1983, larvae were established on trees 6 weeks prior to treatment with conidia or resting spores. These larvae were concealed in the foliage, but it was possible to infect them with some of the treatments (D.F. Perry, personal communication).

An experimental inoculum has been produced from mycelial mats of *E. radicans* grown in culture, dried and ground to a fine powder (Soper 1985). This product was tested on potted balsam fir trees and a field trial was conducted in Maine in 1983 when it was applied on fourth, fifth and sixth instar larvae with a mistblower. The mycelia produced conidia and conidial showering was recorded, but infection levels of less than 1 percent were recorded in these tests. It is thought that this disappointing result was due to low spruce budworm population densities and to cool temperatures following application. A search is now being made for a cold-tolerant strain of the fungus.

Currently, there is interest in modeling both the potential impacts of fungal treatments on spruce budworm and the interrelationships between naturally occurring pathogens (fungi and protozoa), parasites (*Apanteles* and *Glypta*), and the environment (Perry and Whitfield 1984; D.F. Perry and J. Régnière, personal communication). There is still considerable interest in developing Entomophthorales and research is focused on mass production, epizootiology, and treatment strategies. In addition, fungi which are not natural pathogens of spruce budworm are also being evaluated. Several imperfect fungi are registered around the world as mycoinsecticides and are commercially available. A large screening program has been established for these species of fungi which can readily be mass produced. This screening, in conjunction with developmental studies and process modeling, will serve as a basis for well planned field trials in the future.

Viruses

Four different types of insect viruses have been isolated from nine different *Choristoneura* spp. These include six nuclear polyhedrosis viruses (NPV), four granulosis viruses (GV), four entomopoxviruses (EPV) and one cytoplasmic polyhedrosis virus (CPV). Generally, all these viruses appear to be cross infectious to the spruce budworm and the western spruce budworm, although all the permutations of cross-infectivity tests have not been conducted. Naturally occurring virus epizootics have not been observed to date in spruce budworm or western spruce budworm populations, and this is discouraging when one is contemplating the development of a virus as a biocontrol agent.

NPVs and GVs are classified as Baculoviruses and Baculoviruses have only been found in arthropods. Most research has been conducted on *C. fumiferana* NPV, but field trials have also been conducted with *C. occidentalis* GV and 2-year cycle spruce budworm (*C. biennis*) EPV. On some occasions combinations of viruses were sprayed, not by choice, but because contamination had occurred during virus production. Extensive safety tests of spruce budworm NPV have been conducted in mammals and birds and no ill effects were observed (Valli et al. 1976).

Viruses only grow in living cells, so they have to be propagated either in susceptible insect larvae or in cell cultures. *C. fumiferana* NPV will grow in cell culture (Arif et al. 1976), but, presently, it is not economically feasible to produce the quantities required for field trials and insect larvae are used. *C. fumiferana* larvae were originally used for virus production, but since 1981, mainly *C. occidentalis* larvae have been used. The western species is more susceptible to both NPV and GV (Cunningham et al. 1983a), less inoculum is required, there is less loss to pupation, and less silk is spun in rearing cups facilitating faster harvesting. However, even *C. occidentalis* larvae are not an ideal host for virus production. Larvae are small and a sixth instar larva, heavily infected with NPV yields only 5×10^8 polyhedral inclusion bodies (PIB). A search for a larger host insect for virus production has proved unsuccessful to date. *C. fumiferana* NPV infects neonate larvae of cabbage looper (*Trichoplusia ni*), and wax moth (*Galleria mellonella*), but it does not infect large larvae which are required for virus production (Stairs et al. 1981). Attempts to use saltmarsh caterpillar (*Estigmene acrea*) for production of *C. fumiferana* NPV were also unsuccessful (Shapiro et al. 1982).

Field trials with viruses have been conducted on both spruce budworm and western spruce budworm but much greater emphasis has been placed on the former species. First field trials were conducted in 1959 and 1960 when small trees in Ontario were sprayed with NPV and GV (Stairs and Bird 1962), and in 1969 a range of dosages of NPV was applied on individual trees at 2- to 3-day intervals throughout the larval period (Bird and McPhee 1970). In 1970, an EPV isolated from 2-year cycle spruce budworm (*C. biennis*) (Bird et al. 1971), gave high levels of mortality in the laboratory at much lower dosages than viruses previously tested and it was thought that this EPV would be an effective biocontrol agent.

The first aerial spray trials with viruses were conducted in 1971 and both EPV and NPV were tested (Bird et al. 1972). The EPV that was applied was contaminated with low levels of both NPV and CPV and the NPV was contaminated with CPV. In 1972, pure EPV was applied, but in that year it was found that carry-over of NPV from one year to the next was much better than with EPV and further trials with EPV were suspended. From 1973 onward, most efforts were concentrated on developing NPV as a viral pesticide and only two plots have been sprayed with GV. Between 1971 and 1983, 62 plots with a combined area of 2 585 ha (6,388 acres) were sprayed with viruses to control spruce budworm and a further 3 plots with a combined area of 72 ha (178 acres) were sprayed with chemical insecticides followed by viruses (Cunningham 1982, 1985; Cunningham and Howse 1984).

In trials with NPV, the following parameters have been studied: timing of application, dosage, tank mixes, spray equipment and droplet size, impact on different species of host trees, and persistence of virus from one year to the next. Applications have been made on second instar larvae as they emerge from hibernacula and at budflush on fourth, fifth, and sixth instar larvae. Treating second instar larvae is an attractive strategy as they are highly susceptible, there is time for secondary infection to occur, there may be foliage protection and, if there is a hardwood overstory, it has not flushed. However, timing of application is critical and emergence may be over a long period if the weather is cool. Out of four attempts to treat emerging second instar larvae, only one was considered to have been timed correctly. At budflush, larvae are exposed and eating voraciously. Dead larvae add high levels of polyhedra to the inoculum pool, which may have an impact the following year. Dead larvae and pupae remain overwinter on the foliage and still contain viable virus the next season. Viruses are relatively slow acting and when applied at budflush, there is not time for secondary infection to occur. Only those larvae that ingest a lethal quantity of the spray deposit will die. Also, there is little or no foliage saved when viruses are applied at budflush.

Dosages of NPV tested have ranged from 2×10^{10} polyhedral inclusion bodies (PIB)/ha to a double application with 3.4×10^{12} followed by 2.3×10^{12} PIB/ha. The most commonly used dosage has been 7.5×10^{11} PIB/ha which, on some occasions, has given acceptable levels of population reduction. A variety of tank mixes and stickers has been tested and, until recently, most were aqueous and contained 25 percent v/v molasses. Since 1982, an emulsifiable oil (Dipel® 88 blank carrier vehicle) has been used, with the virus applied in 25 percent oil and 75 percent water. Emitted volumes have ranged from 4.5 to 28.2 L/ha (½ to 3 gal/acre) with most applications made at 9.4 L/ha (1 gal/acre). Both boom and nozzle and Micronair® rotary atomizers have been used and generally coarse droplets with a stain diameter of 200 to 400 microns on Kromekote® cards have given better results than droplets with a diameter of less than 100 microns. When the impact of treatments has been monitored on larvae from both balsam fir and white spruce hosts, generally better results are obtained on white spruce.

Carry-over of virus from one year to the next has been recorded in some plots, but rarely at a sufficient level to give acceptable population regulation. Best levels of carry-over followed the first aerial application of NPV in 1971 on two mature white spruce stands that were monitored annually until 1977. Significant levels of NPV were recorded until 1976; the population of spruce budworm declined drastically in 1977. Although results were not spectacular, the virus probably exerted sufficient control of the spruce budworm population to reduce defoliation and thereby prevent tree mortality (Cunningham et al. 1975; Cunningham and Howse 1984). Subsequent attempts to repeat this experiment and duplicate the results have been unsuccessful.

The same viruses which infect spruce budworm also infect western spruce budworm. When the pathogenicity of NPV and GV was tested in both species, western spruce budworm was considerably more susceptible to both viruses and it appeared to be a better candidate for regulation with viruses than the eastern species (Cunningham et al. 1983a). Ground spray trials in British Columbia in 1981 indicated that GV had a greater impact than NPV at low dosages on western spruce budworm (Cunningham et al. 1983b). Similar trials were conducted in the United States (M.J. Stelzer and D.W. Scott, personal communication). They found no significant difference between three dosages of NPV and GV applied at two different times and they felt that neither virus warranted further development.

Aerial spray trials with viruses were conducted on western spruce budworm in British Columbia in 1976, 1978, and 1982 and six plots with a total area of 424 ha (1,048 acres) were treated. Following application of NPV at 7.5×10^{11} PIB/ha in 1978 on three plots, 25, 55 and 87 percent of larvae were infected at 15 days post-spray (Hodgkinson et al. 1979). In 1979 and 1980 surveys were conducted on two of these plots; in 1979 levels of NPV infection were recorded as 18 and 54 percent and in 1980 as 7 and 17 percent. Populations declined in 1979 in the treated plots compared to the check plots, but this trend was reversed in 1980 (Shepherd et al. 1982).

In 1982, a 172-ha (425-acre) plot was treated with NPV and a second 172-ha (425-acre) plot with GV at budflush when western spruce budworm larvae were at the peak of the fourth instar. The two viruses were compared on the basis of weight and 9 kg (20 lb) of lyophilized, virus-infected larval material was applied to each plot; the actual dosage of NPV was 5.4×10^{11} PIB/ha and the dosage of GV was 1.7×10^{14} capsules/ha. The aim of the experiment was to achieve population regulation by virus carry-over from one year to the next. The NPV had a greater impact than the GV in the year of application with 52 percent population reduction due to treatment compared to 35 percent for GV. In samples of larvae reared individually in the laboratory 66 to 80 percent died from NPV and 59 to 62 percent from GV. The impact of both viruses was less in 1983 than in the year of application with population reduction attributed to NPV carry-over at 35 percent and GV at 15 percent (I.S. Otvos, J.C. Cunningham and W.J. Kaupp, unpublished). These results were disappointing and it is considered that relying on virus carry-over from one year to the next to regulate western spruce budworm is not a feasible strategy.

In spite of intensive research for more than a decade, use of viruses as biocontrol agents for spruce budworms can only be regarded as experimental and operational use appears unlikely in the near future. The search for new, more pathogenic viruses continues along with a search for larger hosts for virus production. Improved tank mixes with better stickers and UV protectants may keep the virus in a viable state on foliage for longer periods of time, making application before emergence of second instar larvae a feasible strategy. The epizootiology of spruce budworm viruses has not been well studied and investigation in this area may yield the answer as to why results of virus applications have often been less than satisfactory. The most exciting aspect of current spruce budworm virus research is that of recombinant DNA technology. Considerable progress has been made in constructing a physical map of the genome of *C. fumiferana* NPV (Arif and Doerfler 1983, 1984). The next step is to ascribe functions to different segments of the DNA and hopefully manipulate such factors as virulence, host range, and resistance to UV light.

Protozoa

The microsporidian parasite, *Nosema fumiferanae*, is prevalent in long established outbreaks of spruce budworm and can reach a level at which about 80 percent of the insects are infected (Wilson 1981, 1982a). This parasite is comparatively rare in western spruce budworm (J.C. Cunningham, unpublished). *N. fumiferanae* retards larval and pupal development and reduces pupal weight, fecundity, and longevity of adult moths. It is transovarially transmitted (Thomson 1958; Wilson 1977, 1982b). Chronic rather than acute disease generally results from infection with *N. fumiferanae*, although some larval mortality can occur. Another microsporidium, *Pleistophora schubergi*, occurs only rarely in spruce budworm populations but is considerably more pathogenic than *N. fumiferanae*. The LD_{50}, with 95 percent confidence limits, on fourth instar larvae for *N. fumiferanae* is 2.8×10^6 ($3.0\text{-}2.5 \times 10^6$) spores/larva and for *P. schubergi* is 2.3×10^4 ($7.3 \times 10^4 — 3.4 \times 10^3$) spores/larva (G.G. Wilson, personal communication).

Protozoa only replicate in living cells and the same problems occur with their mass production as with viruses. Growing them in cell cultures has been investigated (Sohi and Wilson 1976; Kurtti and Brooks 1977), but this is not economically feasible so the host insect or an alternative susceptible species has to be used for propagation. *N. fumiferanae* can be propagated in forest tent caterpillar (*Malacosoma disstria).* *P. schubergi* has a wide host range which also includes forest tent caterpillar.

Small-scale field trials were conducted with both *N. fumiferanae* and *P. schubergi* in 1975 and 1976 (Wilson and Kaupp 1975, 1976a, 1976b). Individual white spruce and balsam fir trees were treated in 1976 when larvae were in the fourth and fifth instars. With *N. fumiferanae*, levels of infection increased by 30 percent in larvae on white spruce hosts and 35 percent on balsam fir hosts; with *P. schubergi*, the figures were 48 percent and 95 percent, respectively. A survey of the same trees the following year showed that the incidence of *N. fumiferanae* infection remained the same on the treated trees, but the incidence of naturally occurring infection in larvae on untreated check trees increased. *P. schubergi* was found in only 3 percent of larvae in spite of the initial high infection levels in the year of application (Wilson 1978).

At present, there are no plans to develop microsporidia for spruce budworm control but there is considerable interest in assessing the impact of *N. fumiferanae* as a natural mortality factor because of its prevalence in spruce budworm populations. The influence of microsporidia on other control agents, both chemical and biological is another important aspect which merits further research. It is not known if susceptibility to chemical insecticides is altered by the presence of microsporidia in larvae. However, it has been suggested that microsporidian infection enhances the effect of B.t. (Smirnoff 1963, 1971), and preliminary tests have shown that application of NPV on larvae infected with *N. fumiferanae* gives higher mortality than on uninfected larvae (J.C. Cunningham, unpublished).

Insect Growth Regulators

Insect physiologists have searched for materials that block critical biochemical pathways unique to insects and which are safe to other life forms. Currently, two such systems, both recognized quite fortuitously, have been developed as control agents. These are juvenile hormone mimics and benzoylphenyl ureas. Juvenile hormones, in combination with other endocrine secretions control growth, moulting, and development. If the level of juvenile hormone is low in the final larval instar, pupation occurs, but if it is high then the moult results in a larval-pupal mosaic which, under most conditions, dies. Synthetic analogs have been discovered, which are more active than the naturally occurring hormone, and over 500 have been synthesized. Juvenile hormones are most effective on insect species that cause damage as adults. When applied on defoliating insects such as spruce budworm, the impact of the treatment will not be evident until the following year (Retnakaran et al. 1982). Antijuvenile hormones are chemicals which negate the activity of juvenile hormones. When applied, for example, on early instar milkweed bugs, they moult into miniature sterile adults instead of the next larval stage (Bowers 1976). Fluormevalonate is a potent antijuvenile hormone (Quinstad et al. 1981), but at present, no antijuvenile hormone is being developed commercially.

Around 1970, it was found that benzoylphenyl ureas being developed as herbicides by the Philips Duphar Company had insecticidal activity; they disrupted the normal moulting process. This led to the development of Dimilin® (also called PH60-40 and diflubenzuron) which was the first moult inhibitor to be commercialized. Benzoylphenyl ureas inhibit the polymerisation of chitin. The integument fractures and ruptures during moulting, which leads to death of the insect.

The first field trials with insect growth regulators on spruce budworm were conducted in New Brunswick in 1972. Two juvenile hormone analogs, C28204 and GS42710 (Ciba Geigy), were sprayed on caged fifth instar larvae and results were considered to be sufficiently encouraging to warrant further testing. In 1973, compounds GS42710 and CGA13353 were aerially sprayed twice, at the peak of the fifth instar and at the peak of the sixth. Both compounds affected spruce budworm survival to the adult stage and CGA13353 possibly affected mating behavior and oviposition. The treatments did not save any current year's foliage (Outram 1975).

Following laboratory and greenhouse tests, aerial spray trials with insect growth regulators were conducted in Ontario in 1974 (Retnakaran et al. 1977). Two juvenile hormone analogs, ZR515 also known as Altosid or methoprene (Zoecon Corp.) and RO-103108 (Dr. Maag, Ltd.), and Dimilin® were tested. After further testing on spruce budworm in Ontario in 1975, 1976 and 1977, it was concluded that juvenile hormone analogs were not effective for saving current year's foliage and attention was focused on moult inhibitors (Retnakaran et al. 1978).

Other species of insects such as the white-marked tussock moth and forest tent caterpillar were found to be much more susceptible to Dimilin® than the spruce budworm or western spruce budworm. The reason for these differences has been explained by different rates of absorption and metabolism with the more sensitive species absorbing more and metabolising less diflubenzuron than the refractive species (Retnakaran et al. 1980; Granett et al. 1980).

No field trials have been conducted with insect growth regulators on western spruce budworm but several compounds have been screened in the laboratory and some compare favorably to chemical insecticides. Tests with juvenile hormone analogs are described by Robertson and Kimball (1979a, 1981). Reduction in fertility and fecundity were also noted (Robertson and Kimball 1979b). Tests with moult inhibitors are reported by Gillette et al. (1978), Robertson and Haverty (1981, 1982) Rappaport and Robertson (1981), and Robertson (1982).

A total of 25 insect growth regulators has been screened against the spruce budworm (A. Retnakaran, personal communication). Older larval instars were found to be more susceptible to Dimilin® than younger ones (Retnakaran and Smith 1975; Granett and Retnakaran 1977) and since this discovery all new compounds have been tested on a range of larval instars. Brushwein and Granett (1977) showed that certain moult inhibitors such as EL 494 (Eli Lilly and Co.) when fed to sixth instar spruce budworm larvae caused reproductive failure in surviving adults, but survivors of Dimilin® treatments produced a normal complement of progeny.

Dimilin® was tested again in Ontario in 1977 along with PH 60-41 (also a Philips-Duphar compound) and EL 494. In 1978, Dimilin® was tested for the last time along with EL 495 and BAY SIR 8514 (Chemagro Ltd.); in 1979, BAY SIR 8514 was compared to the chemical insecticide Matacil®; and in 1980 BAY SIR 8514 and UC 62644 (Union Carbide) were compared to Matacil® and Dipel® 88 (*Bacillus thuringiensis*) (Retnakaran 1980, 1981, 1982). Retnakaran concluded that Dimilin®, even at 280 g/ha (4 oz/acre), is not a very effective compound for spruce budworm control and poor results were also obtained from trials conducted in Maine (Dimond 1975). EL 494 appears to break down fairly rapidly in the environment and results with it have been considered unsatisfactory. BAY SIR 8514 is reasonably active on spruce budworm, but it is slow acting and foliage protection is poor following an application. UC 62644 is by far the most promising compound tested to date. At 35 g/ha (½ oz/acre) and 70 g/ha (1 oz/acre) it is comparable to single and double dosages of Matacil® at 70 g/ha (1 oz/acre) in terms of both population reduction and foliage protection. Both were applied at emitted volumes of 4.7 L/ha (½ gal/acre). The UC 62644 wettable powder was suspended in Sunspray® 7N oil which had excellent deposit characteristics and the Matacil® was formulated in 585 oil.

It has been shown in the laboratory that the reproductive potential of spruce budworm surviving a UC 62644 treatment can be reduced. Concentrations that are not lethal to treated sixth instar larvae and subsequent pupae can cause changes in emerging adults. Reduction in mating success was greater in treated males and reduction in egg production was significant only when females were treated (Madore et al. 1983).

The safety of Dimilin® was questioned by the Environmental Protection Agency (EPA) in the United States. Long-term chronic toxicology studies have recently been completed; no hazardous effects were noted and it has been declared a totally acceptable pest control agent. UC 62644 is now referred to as CGA112913 (Ciba Geigy) and 2-year chronic toxicology studies are underway (A. Retnakaran, personal communication). It is hoped that this compound will be commercially available in the not-too-distant future.

Since Dimilin® was introduced in 1973 by Philips-Duphar, several other companies have developed moult-inhibiting insect growth regulators. Eli Lilly, Gulf, Union Carbide, Monsanto, Velsicol, Stauffer, Dow Chemical, Nutrilite Products, Upjohn, and Zoecon are some of the companies holding patents for insect growth regulators. The successful outcome of the long-term toxicology studies on Dimilin® has stimulated commercial interest in this group of compounds. Development of an agent for control of spruce budworm alone is not considered to be economically feasible, and it would have to be effective for control of major agricultural pests as well before a company would consider registration and commercialization.

The use of insect growth regulators is preferable to broad spectrum chemical pesticides; IGRs have little adverse effect on nontarget beneficial insects such as parasites, predators and pollinators and they are safe to vertebrates (Wilcox and Coffey 1978; Maas et al. 1980; Retnakaran et al. 1985).

Sex Pheromones

Most of the important behavioral activities of insects are controlled by odorous chemical messengers called semiochemicals. These chemicals include sex pheromones, which are transmitted from one member of a species to another to initiate and control mating behavior. In spruce budworm, the sex pheromone is released into the atmosphere from a gland near the genitalia of the female and, as it evaporates, it is carried downwind and diluted. The pheromone is detected by males, which have thousands of olfactory cells on their antennae, and they respond by flying upwind, following the plume of pheromone molecules to the vicinity of the female. Then, still under the influence of the pheromone, courting and mating are performed.

In general, pheromones are nontoxic and highly specific for target insects. Pheromone-baited traps have proved to be a most useful tool for monitoring populations of many species of insects. In easily accessible areas enough traps can be used to remove sufficient males so that few females mate. This technique is called trapping out, but it is not feasible for an insect as widespread as the spruce budworm. An alternative method of preventing insects from mating is called the male confusion or mating disruption technique. The atmosphere is permeated with synthetic pheromone which the male cannot distinguish from female-produced pheromone. Then the males cannot locate the females. The use of pheromones for spruce budworm control has been reviewed by Sanders and Seabrook (1982) and Silk and Kuenen (1984).

The main component of the sex pheromone of the spruce budworm was identified as *trans*-11-tetradecenal which is an aldehyde (Weatherston et al. 1971), but trapping results with commercial preparations were inconsistent and it was found that a blend of two isomers are the main components. They have been identified as *trans* (E)- and *cis* (Z)-11-tetradecenal in the ratio of approximately 95:5 (Sanders and Weatherston 1976; Silk et al. 1980; Jennings and Houseweart 1983b). Additional minor components have also been identified in the effluvia from the female's pheromone gland (Silk et al. 1980), but their role has not been demonstrated (Alford et al. 1983; Sanders 1984). Although Sanders (1979a) found that the 95:5 blend evoked full courtship behavior, Alford et al. (1983) did not. However, it is agreed that the male response to female moths is better than to synthetic pheromone, which suggests that an important component is still missing (Alford et al. 1983; Sanders 1984).

To date, all field trials to regulate populations of the spruce budworm by the confusion technique have involved only the (E:Z)-11-tetradecenals. Disruption of male attraction to natural sex pheromone is highest with the 95:5 blend (Sanders 1981). Commercial preparations of the E:Z blend (94:6) have been called Fulure. It is imperative that the pheromone is released at an effective concentration for the entire length of time that male adult moths are present.

The first trial was conducted in Ontario in 1975 and the pheromone, in microcapsules, was applied to 12 ha (30 acres) of spruce-fir forest at a rate of 7.4 g AI/ha (0.10 oz AI/acre). A 97 percent reduction of catch in pheromone traps was recorded (Sanders 1976). In 1977 in Ontario, Conrel® hollow fibres were applied at about 3 and 30 g AI/ha (0.04 and 0.42 oz AI/acre) on two 10-ha (25-acre) plots with low population densities and at about 5 g AI/ha (0.07 oz AI/acre) on a 250-ha (618-acre) plot with a moderate population density. In all three plots the reduction in trap catch compared to untreated check areas was greater than 97 percent but attempts to demonstrate population reductions were inconclusive (Sanders 1979b).

In 1978, four concentrations, ranging from 0.2 to 40 g AI/ha (0.003 to 0.56 oz AI/acre), were tested in New

Brunswick and Nova Scotia using Conrel® hollow fibres. Unfortunately the active ingredient evaporated too quickly indicating that there was a problem with the formulation (Weisner et al. 1980). However during the period, the pheromone was detectable and trap catches were significantly reduced. With caged insects, there was a significant reduction in the numbers of females mated in the presence of the pheromone with effects being greatest at the lowest population densities (Schmidt et al. 1980).

In 1980, a formulation of pheromone in Hercon® flakes was tested in Maine with dosages of 28, 52, and 516 g AI/ha (0.39, 0.74, and 7.3 oz AI/acre). Results were marred by a heavy invasion of gravid females from other areas (Dimond et al. 1984). Hercon® flakes were tested again in Ontario in 1981 with 100 g AI/ha (1.4 oz AI/acre) applied on a 30-ha (74-acre) white spruce plantation. Reduction in trap catches was 90 percent and reduction in mating among caged moths was 40 percent. In this case results were obscured by a population decline attributed to disease (Sanders and Silk 1982).

Early field tests showed that western spruce budworm males responded well to (E)-11-tetradecenal (Weatherston et al. 1971), but subsequent work has shown that the pheromone is closer to a 92:8 blend of the E and Z isomers (Cory et al. 1982; Silk et al. 1982). Hercon® flakes were tested on western spruce budworm in 1979 in Oregon. Dosages of 2, 8, 32, and 128 g AI/ha (0.03, 0.11, 0.45 and 1.8 oz AI/acre) were each applied on replicated 10-ha (25-acre) plots. The synthetic pheromone had an 88:12 E:Z ratio which is slightly different than the blend identified from female emissions. The formulation released pheromones too rapidly during the first week following application and 55 percent of it had dissipated after 7 days. Reduction of males in traps was recorded in all treatments, but they were not totally suppressed by even the highest dosage (G.E. Daterman et al. 1985).

Evidence from other lepidopterans shows that the effectiveness of pheromones for disrupting mating decreases as population density increases. However, mating has been reduced by up to 80 percent in high density caged populations of spruce budworm by high concentrations of synthetic pheromone (Schmidt and Seabrook 1979; Schmidt et al. 1980; Ross et al. 1982; Palaniswamy et al. 1982). None of the aerial spray trials on uncaged populations has yielded conclusive results. However in all instances, the chemicals had a profound effect on male behavior causing a dramatic reduction in the numbers of male moths caught in traps. Unfortunately there was no conclusive proof of a reduction in mating or in the number of fertile eggs. The inability to detect such effects may lie partly in experimental designs which allowed immigration of female moths from outside the treated areas. Shortcomings in the formulations may also be partly to blame.

Satisfactory release rates of pheromone in the laboratory do not necessarily mean the anticipated levels of pheromone will be achieved in the air in the forest. Environmental factors affect release rate, chemical breakdown, and adsorption of the active materials. However, development of new techniques of detecting the chemical in air samples facilitates checking the amount of chemical in the air space (Weisner and Silk 1982). A very elegant method has recently been devised to measure pheromone release rates and concentration in the atmosphere. A novel bioluminescence assay uses bacterial luciferase to quantify aldehyde sex pheromones (Meighen et al. 1981; 1982), and this permits easy, rapid, and accurate measurement of spruce budworm pheromone from trap lures and controlled release formulations used for mating disruption. Airborne pheromone can be trapped on Porapak® Q (Szittner et al. 1982) or in cold traps (Meighen et al. 1983), the latter producing a faster, more sensitive and reproducible system. Release rates as low as 2 nanograms per hour can be measured in less than one hour, making this assay much faster than gas chromatographic methods.

Recent laboratory experiments in a wind tunnel and field experiments have indicated that a strategy of air permeation by numerous low potency emitters is not as effective as fewer, high potency sources (Sanders 1982; Alford and Silk 1983). This implies that males are lured away from females and opens the possibility of mixing chemical insecticides with pheromone formulations. This would improve the effectiveness of the mating disruption treatment by killing the attracted males (C.J. Weisner and P.J. Silk, personal communication).

The full potential of the disruption techniques has still not been adequately evaluated. A well-designed and well-executed field trial, where there is no risk of female invasion, is still required. But before it is undertaken the importance of additional unidentified components must be evaluated and the performance of candidate formulations must be proven under field conditions.

Antifeedants

The chemical composition of plants is a major factor influencing their palatability to insects. Research on compounds that will deter spruce budworm from feeding is in its infancy but a start was made when 110 nonhost plant extracts and 60 naturally occurring chemicals were screened against spruce budworm using a simple assay technique. Only six extracts were classified as highly deterrent. They all came from plants known to contain alkaloids, with the exception of quassin which is extracted from the wood of the Indian neem tree (*Quassia amara*) (Bentley et al. 1982).

Because of their mammalian toxicity, it is unlikely that alkaloids will be used for field applications. However, there are very specific molecular structural requirements which confer deterrent activity and, as more is learned about the relationship between structure and activity, it is hoped that molecules with high deterrent activity and low mammalian toxicity can be designed. The discovery of effective antifeedants would add a new thrust to current spruce budworm regulation strategies (Strunz and Fogal 1981).

The palatability of several species of spruce to spruce budworm varies throughout the year and a substance which is named pungenin, originally found in Colorado spruce, is believed to cause this change (G.M. Strunz, personal communication). If the concentration of this substance could be increased by genetic engineering, it may be possible to develop a strain of trees which is resistant to attack from spruce budworm. This would, of course, be a very long-term project.

Genetic Control

In some situations the release of sterile adults has been used successfully to control or reduce populations of insect pests. The sterile insect technique involves the mass rearing of sterile or artificially sterilized insects and releasing them in sufficient numbers to compete with wild insects and reduce their reproductive potential. The most notable example is control of the screw worm in southwestern United States and northern Mexico (Davidson 1974). There have also been programs to control a number of fruit flies, mosquitos, tsetse flies, cotton boll weevils, and codling moth (LaChance 1979). Some preliminary experiments have been undertaken to examine the procedures and ascertain the feasibility of using this technique to regulate spruce budworm populations.

To develop a sterile insect release program, a genetic control system appropriate for the target insect must be found, the released insects must remain competitive and there must be a method of detecting released males so as to monitor their dispersion and evaluate the impact. A major concern is that laboratory-reared insects may differ from feral males in some way which decreases the effectiveness of the release.

Thiotepa and cobalt $(Co)^{60}$ irradiation have been shown to effectively sterilize male spruce budworm (Retnakaran 1970, 1971). Males sterilized by Thiotepa are more competitive than normal males and can suppress fertility of caged laboratory populations by up to 90 percent. However, fertility of field populations was not reduced because adult mating behavior was adversely affected. Males irradiated with 20 to 30 kR of Co^{60} are fully sterile but noncompetitive. However, treatment with 2 to 5 kR reduces fertility by about 40 percent and does not affect their competitive ability. Offspring of these males are likely to have a sex ratio biased to more males than females; they have reduced viability and are almost completely sterile (Ennis 1979; T.J. Ennis, personal communication).

Pheromone traps have been used to monitor simulated release experiments. The released males were marked with a light dusting of fluorescent dye. Up to 41 percent of released laboratory-reared males were recaptured. Some were treated with 2 kR Co^{60} and this genetically effective dosage appeared to have little effect on short-range flight in the field (Ennis and Charlebois 1979). The use of pheromone traps containing a sterilant is an interesting concept. Although an actual sterilant has not been employed, a study was conducted to record numbers of male moths visiting pheromone traps containing marking dye. Males were subsequently recaptured in sticky pheromone traps. In a simulated autosterilization test 2 to 17 percent of feral males captured had previously visited pheromone-baited stations (T.J. Ennis, personal communication).

Successful genetic control of any forest insect pest has yet to be demonstrated and spruce budworm is probably one of the most difficult candidates. Its potential, if any, lies in the integrated control of low level populations to prevent outbreaks (Ennis 1981). This line of research is not currently being pursued.

Conclusions

After the collapse of the European spruce sawfly population which was caused by imported parasites and a virus in the 1940s and early 1950s, it was believed that similar methods could be used to reduce the status of the spruce budworm to that of an insignificant forest insect. We are no closer to that ideal solution than we were 35 years ago but that is not to say that an ideal solution does not exist. An overlooked or undiscovered self-replicating organism, which is capable of regulating spruce budworm populations, may exist either in North America or in some obscure corner of the world. Although the ultimate solution remains to be discovered, a great deal of progress has been made in the development of biorationals.

Western spruce budworm in British Columbia appears to be a better candidate than the eastern species for testing novel control strategies. Unlike the spruce budworm, it occurs in isolated pockets along river valleys and not over vast continuous areas. These pockets, or ecological islands, can be treated with biorationals with little possibility of reinvasion from neighboring infestations. However, the economic importance of western spruce budworm is less than that of the eastern species and consequently less research has been conducted on it. Perhaps control strategies could first be tested on western spruce budworm and, if successful, then be applied on the eastern species.

Integrated pest management (IPM) has been strongly promoted as a means of solving insect pest problems (Newsom 1980). The first steps in an IPM program are a thorough knowledge of the biology and population dynamics of the pest and an assessment of its impact on the host so that an economic damage threshold can be defined. An intelligent decision can then be made on the type of remedial action to be implemented. Efficient methods of monitoring the pest population are fundamental to any pest management strategy: methods of monitoring spruce budworm populations have been well developed and are applied through most of the range of this insect. Sanders (1980) has compiled a summary of methods used to sample outbreaks (epidemic populations). Pheromone traps may prove to be extremely useful for monitoring endemic populations (Sanders 1978).

The current spruce budworm management philosophy emphasizes learning to tolerate the spruce budworm and to manage our forests in concert with this pest. With accurate survey and monitoring techniques, predictions can be made regarding mortality of mature stands of trees that are ready to be harvested. If these stands are accessible and the intention is to harvest them before they become overmature and die, two courses of action can be taken. The trees can be harvested before, or soon after, they are killed by spruce budworm or they can be sprayed with a chemical or biorational pesticide for several consecutive years until harvested.

There are two other reasons why it may be necessary to regulate spruce budworm and prevent tree mortality. The first is the aesthetic and recreational aspect; tourists, hikers, and sportsmen avoid forests of dead trees. The second is the fire hazard associated with budworm-killed stands. These two problems are most evident in areas where there are large stands of pure balsam fir than in areas of mixed forest type containing only some balsam fir.

A forest manager, therefore, requires methods of regulating spruce budworm populations for a variety of reasons. There are several broad spectrum organophosphate and carbamate pesticides registered for spruce budworm control, the most widely used being fenitrothion, Matacil® and Sevin®. Synthetic pyrethroids, which are extremely safe to birds and mammals, are rarely used in aerial forest spray applications because of their high level of toxicity to fish. All these broad spectrum chemical insecticides have an adverse effect on beneficial insects such as parasites, predators, and pollinators. There is only one biorational pesticide, registered for spruce budworm control and that is B.t. There are three companies in North America producing B.t. and problems of availability seem unlikely. There is no evidence of forest insects becoming resistant to B.t. and no reports of undesirable side effects following the use of B.t. However, having only one operational option to the use of chemical pesticides is not enough. Others must be developed.

In the last decade, considerable progress has been made in the use of B.t. for spruce budworm control and it is becoming more acceptable to forest managers as an alternative to chemical insecticides. Research on B.t. for control of western spruce budworm has lagged behind research on the eastern species; there is less economic pressure to develop biorationals for western spruce budworm control and it is sometimes difficult to obtain effective aerial spray deposits on the mountainous and dry terrain in which this species is usually encountered. The greatest improvement in the use of B.t. for spruce budworm control has been the development of high potency formulations that can be applied undiluted in similar volumes to chemical pesticides. The benefit of these high potency formulations is two-fold. Firstly, with less volume per unit area, the application costs are reduced and, secondly, they are more efficacious because of the increased dosage of crystals and spores per droplet. There is a strong possibility that the effectiveness of B.t. will be further enhanced by the selection and commercialization of more lethal strains and by genetic engineering.

It is predictable that the next biorational pesticide which will become available for widespread use will be a moult inhibitor. Development of these agents has been delayed because of questions regarding the safety of Dimilin®. However, long-term chronic toxicology studies of Dimilin® have recently been completed and no problems were encountered. This has stimulated commercialization of other moult inhibitors including CGA 112913 which is highly effective against spruce budworm. Two-year chronic toxicology studies are underway for this compound, which is also effective against some major pests of cotton.

Other biorational pesticides are only at the experimental stage of development but could, perhaps, be applied on high value stands where the cost of treatment is not such a critical factor as on naturally regenerated forest. The use of sterile male releases and application of protozoa have, at this time, been discounted as being impractical. Viruses and fungi have tremendous potential in theory, but effective products have yet to be developed. Male confusion using pheromones is a viable concept and it could be used over limited areas once problems involving attractiveness of the pheromone, formulation, and application technology have been resolved. Inundative releases of *Trichogramma minutum*, although presently expensive, are an interesting technique for small, high value areas. Development of an artificial substrate to replace insect eggs for mass rearing of *Trichogramma* could reduce costs dramatically. Research on nematodes and antifeedants is at too early a stage of development for comment.

Some strategies would have a greater impact on low to moderate population densities than on outbreak populations of spruce budworm. Hence in an IPM program, they could be applied after another agent, chemical pesticide, B.t., or an insect growth regulator had been used to substantially reduce the initial population. Pheromones may play a useful role here. Possibly a *Trichogramma* release could be used to further reduce the spruce budworm population density. Provided that there is no reinvasion of the treated areas, there could be protection for several years without further treatment. Scientists can devise a variety of integrated pest management strategies but most will appear unacceptable to forest managers because of cost. However, once a method is proved to be operationally feasible and gives acceptable results, there is always a possibility that further research and improved technology can reduce these costs dramatically.

The most exciting recent development in biological sciences has been in recombinant DNA technology. The possibilities are limitless. The genetic manipulation of B.t. and Baculoviruses are currently receiving attention. The development of new, improved strains in the not-too-distant future is a distinct possibility. There is evidence that the gene for the B.t. toxin is on a plasmid and this has stimulated a great deal of interest and effort toward engineering improved forms of the crystal. It is conceivable that the toxin gene can be introduced into the genetic material of plants rendering them toxic to leaf-eating lepidopterans. It would be 50 to 70 years until genetically engineered seed would yield budworm resistant trees. However, such long-term strategies should not be arbitrarily discounted.

Viruses, have the simplest genome of any life form and are obvious candidates for genetic manipulation. However, Baculoviruses, compared to many other viruses, have larger and more complex genomes which code for more than 30 proteins. Considerable progress has been made in constructing a physical map of the spruce budworm NPV genome (Arif and Doerfler 1983, 1984) and the next step is to produce a transcriptional map which ascribes functions to different regions of the DNA (B.M. Arif, personal communication). It is conceivable that the virulence, host range, and resistance to inactivation by UV light can be altered once the genes controlling various viral functions are identified.

With the exception of B.t., there has been little interest in commercialization of microbial control agents to date and almost all the research and development of such agents has been conducted at government and university laboratories. Recently, several companies have been formed which aim to market technology in the genetic manipulation of biological control agents and to replace conventional chemical pesticides with biological control agents. It is too early to judge how successful these enterprises will become or their impact on the well established pest control products market. The next decade promises to be a most exciting one in the field of insect pest management.

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Literature Cited

Alford, A.R.; Silk, P.J. 1983. Effect of pheromone-releaser distribution and release rate on the mating success of spruce budworm (Lepidoptera: Tortricidae). J. Econ. Entomol. 76:774-778.

Alford, A.R.; Silk, P.J.; McLure, M.; Gibson, C.; Fitzpatrick, J. 1983. Behavioral effects of secondary components of the sex pheromone of the eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 115:1053-1058.

Anderson, J.F. 1976. Egg parasitoids of forest defoliating Lepidoptera. Pages 233-249 *in* J.F. Anderson and H.K. Kaya, eds. Perspectives in Forest Entomology. Academic Press, New York.

Arif, B.M.; Doerfler, W. 1983. Characterization of the DNA from *Choristoneura fumiferana* nuclear polyhedrosis virus. J. Bact. Hyg. A254:147-148.

Arif, B.M.; Doerfler, W. 1984. Identification and localization of reiterated sequences in the *Choristoneura fumiferana* MNPV genome. EMBO J. 3:525-529.

Arif, B.M.; Sohi, S.S.; Krywienczyk, J. 1976. Replication of alkali-released NPV in a cell line of *Choristoneura fumiferana*. Pages 108-112 *in* Proc. 1st Internat. Coll. Invertebr. Pathol. and 9th Annu. Meet. Soc. Invertebr. Pathol., Queen's University, Kingston, Canada.

Armstrong, J.A.; Nigam, P.C. 1975. The effectiveness of the aerial application of Orthene® against spruce budworm at Petawawa Forest Experiment Station during 1974. Can. For. Serv., Ottawa. Inf. Rep. CC-X-82. 29 p.

Beegle, C.C. 1985. The bioassay of *Bacillus thuringiensis* based preparations: historical perspectives and current status. *In* D.G. Grimble and F.B. Lewis, tech. coords. Proc. Symp. Microbial Control of Spruce Budworms and Gypsy Moths. 10-12, April 1984. Windsor Locks, CT. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-100. 175 p.

Bedford, G.O. 1981. Control of the rhinoceros beetle by baculovirus. Pages 409-426 *in* H.D. Burges, ed. Microbial Control of Pests and Plant Diseases 1970-1980. Academic Press, London.

Bentley, M.D.; Leonard, D.E.; Leach, S.; Reynolds, E.; Stoddard, W.; Tomkinson, B.; Tomkinson, D.; Strunz, G.; Yatagai, M. 1982. Effects of some naturally occurring chemicals and extracts of non-host plants on feeding by spruce budworm larvae, (*Choristoneura fumiferana*). Maine Life Sci. Agric. Exp. Stn., Univ. Maine at Orono. Tech. Bull. 107. 23 p.

Bird, F.T.; McPhee, J.R. 1970. Susceptibility of spruce budworm to pure nuclear polyhedrosis virus (NPV) sprays. Can. Dept. Fish. For., Ottawa. Bi-mon. Res. Notes 26:35.

Bird, F.T.; Sanders, C.J.; Burke, J.M. 1971. A newly discovered virus disease of the spruce budworm, *Choristoneura biennis*, (Lepidoptera: Tortricidae). J. Invertebr. Pathol. 18:159-161.

Bird, F.T.; Cunningham, J.C.; Howse, G.M. 1972. Possible use of viruses in the control of spruce budworm. Proc. Entomol. Soc. Ont. 103:69-75.

Bowers, W.S. 1976. Discovery of insect anti-allatotropins. Pages 394-408 *in* L.I. Gilbert, ed. The Juvenile Hormones. Plenum Press, New York.

Brushwein, J.R.; Granett, J. 1977. Laboratory tests of two molting disruptants, EL 494 and Dimilin, against the spruce budworm (Lepidoptera: Tortricidae): mortality and reproductive effects. Maine Life Sci. Agric. Exp. Stn. Univ. Maine at Orono, Misc. Rep. No. 192. 9 p.

Cory, H.T.; Daterman, G.E.; Daves, G.D., Jr.; Sower, L.L.; Shepherd, R.F.; Sanders, C.J. 1982. Chemistry and field evaluation of the sex pheromone of western spruce budworm. J. Chem. Ecol. 8:339-350.

Carrow, J.R., ed. 1983. B.t. and the spruce budworm. Proc. Seminar New Brunswick Dept. Natural Resources, Fredericton, Sept. 1983. 91 p.

Cunningham, J.C. 1982. Field trials with baculovirus: control of forest insect pests. Pages 335-386 *in* E. Kurstak, ed. Microbial and Viral Pesticides. Marcel Dekker, Inc., New York and Basel.

Cunningham, J.C. 1985. Status of viruses as biocontrol agents for spruce budworms. *In* D.G. Grimble and F.B. Lewis, tech. coords., Proc. Symp. Microbial Control of Spruce Budworms and Gypsy Moths. 10-12, April, 1984. Windsor Locks, CT. U.S. Dept. Agric., For. Serv., Broomall, PA, Gen. Tech. Rep. NE-100. 175 p.

Cunningham, J.C.; Howse, G.M. 1984. Eastern spruce budworm viruses: application and assessment. Pages 248-259 *in* J.S. Kelleher and M.A. Hulme, eds. Biological Control of Insects and Weeds in Canada, 1969-1980. Commonw. Agric. Bureaux, Slough, England.

Cunningham, J.C.; Howse, G.M.; Kaupp, W.J.; McPhee, J.R.; Harnden, A.A.; White, M.B.E. 1975. The persistence of nuclear polyhedrosis virus and entomopoxvirus in populations of spruce budworm. Can. For. Serv., Forest Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. IP-X-10. 32 p.

Cunningham, J.C.; Kaupp, W.J.; McPhee, J.R. 1983a. A comparison of the pathogenicity of two baculoviruses to the spruce budworm. Can. For. Serv., Ottawa, Res. Notes 3:9-10.

Cunningham, J.C.; Kaupp, W.J.; McPhee, J.R.; Shepherd, R.F. 1982b. Ground spray trials with two baculoviruses on western spruce budworm. Can. For. Serv., Ottawa, Res. Notes 3:10-11.

Daterman, G.E.; Sower, L.L.; Sartwell, C. 1985. Courtship disruption of western spruce budworm by aerial application of synthetic pheromone. Pages 386-387 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworm research. Proc. CANUSA Spruce Budworms Research Symp., 16-20, Sept. 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Davidson, G. 1974. Genetic Control of Insect Pests. Academic Press, New York. 158 p.

Dimond, J.B. 1972. A demonstration of *Bacillus thuringiensis*, plus the enzyme chitinase, against spruce budworm in Maine. Part 1 Efficacy. Maine Life Sci. Agric. Exp. Stn. Univ. Maine at Orono. Misc. Rep. 144. 34 p.

Dimond, J.B. 1974. Tests of *Bacillus thuringiensis* against spruce budworm in Maine, 1973. Maine Life Sci. Agric. Exp. Stn., Univ. Maine at Orono. Misc. Rep. 153. 23 p.

Dimond, J.B. 1975. *Bacillus thuringiensis* and spruce budworm. Further tests in Maine, 1974. Maine Life Sci. Agric. Exp. Stn. Univ. Maine at Orono. Misc. Rep. 166. 15 p.

Dimond, J.B. 1982. Effects of aerial sprays of undiluted *Bacillus thuringiensis* formulations on spruce budworm. Maine Life Sci. Agric. Exp. Stn. Univ. Maine at Orono. Misc. Rep. No. 274. 9 p.

Dimond, J.B.; Spies, C.J., III. 1980. A comparison of B.t. plus the additives chitinase and Orthene in control of eastern spruce budworm. Maine Life Sci. Agric. Exp. Stn. Univ. Maine at Orono. Misc. Rep. 224. 15 p.

Dimond, J.B.; Spies, C.J., III. 1981. Two-year effects of a *Bacillus thuringiensis* treatment on spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 113:661-663.

Dimond, J.B.; Mott, D.G.; Kemp, W.P.; Krall, J.H. 1984. A field test of mating-suppression using the spruce budworm sex pheromone. Maine Life Sci. Agric. Exp. Stn. Univ. Maine at Orono. Tech. Bull. 113. 21 p.

Dubois, N.R.; Lewis, F.B. 1980. What is *Bacillus thuringiensis*? Pages 233-240 *in* Proc. Annu. Conf. Int. Soc. Arboriculture. Hartford, CT. Aug. 1980.

Dulmage, H.T. 1970. Insecticidal activity of HD-1, a new isolate of *Bacillus thuringiensis* var. *alesti*. J. Invertebr. Pathol. 15:232-239.

Dunphy, G.B.; Nolan, R.A. 1977. Morphogenesis of protoplasts of *Entomophthora egressa* in simplified culture media. Can. J. Bot. 55:3046-3053.

Dunphy, G.B.; Nolan, R.A. 1979. Effects of physical factors on protoplasts of *Entomophthora egressa*. Mycologia 71:589-602.

Dunphy, G.B.; Nolan, R.A.; MacLeod, D.M. 1978. Comparative growth and development of two protoplast isolates of *Entomophthora egressa*. J. Invertebr. Pathol. 31:267-269.

Ennis, T.J. 1979. Detection and isolation of induced chromosome aberrations in Lepidoptera. Experientia 35:1153-1154.

Ennis, T.J. 1981. Genetic control. Pages 134-135 *in* J. Hudak and A.G. Raske, eds. Review of the spruce budworm outbreak in Newfoundland — its control and forest management implications. Can. For. Serv. Submission to the Newfoundland and Labrador Royal Commission on Forest Protection and Management. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Nfld. Inf. Rep. N-X-205.

Ennis, T.J.; Charlebois, N. 1979. A release-recapture experiment with normal and irradiated spruce budworm males. Can. For. Serv., Ottawa. Bi-mon. Res. Notes 35:9-10.

Fast, P.G. 1974. *Bacillus thuringiensis*: its history and mode of action. Dev. Ind. Microbiol. 15:195-198.

Fast, P.B. 1977. *Bacillus thuringiensis* δ-endotoxin: on the relative roles of spores and crystals in toxicity to spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 109:1515-1518.

Fast, P.G. 1981. Measurement of needle area consumed by larvae of *Choristoneura fumiferana*. Can. For. Serv., Ottawa, Res. Notes 1:28-29.

Fast, P.G. 1985. The biochemistry of the crystal protein of *Bacillus thuringiensis*. *In* D.G. Grimble and F.B. Lewis, tech. coords. Proc. Symp. Microbial Control of Spruce Budworms and Gypsy Moths. 10-12, April, 1984. Windsor Locks, CT. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-100, 175 p.

Fast, P.G.; Dimond, J.B. 1984. Susceptibility of larval instars of spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), to *Bacillus thuringiensis*. Can. Entomol. 116:131-137.

Fast, P.G.; Régnière, J. 1984. Effect of exposure time to *Bacillus thuringiensis* on mortality and recovery of the spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 116:123-130.

Finnegan, R.J. 1978. Predation by *Formica lugubris* (Hymenoptera: Formicidae) on *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. For. Serv., Ottawa. Bi-mon. Res. Notes 34:1.

Finney, J.R.; Lim, K.P.; Bennett, G.F. 1982. The susceptibility of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), to *Heterorhabditis heliothidis* (Nematoda: Heterorhabditidae) in the laboratory. Can. J. Zool. 60:958-961.

Gaugler, R. 1981. Biological control potential of neoaplectanid nematodes. J. Nematol. 13:241-249.

Gillette, N.L.; Robertson, J.; Lyon, R.L. 1978. Bioassays of TH 6038 and difluron applied to western spruce budworm and Douglas-fir tussock moth. J. Econ. Entomol. 71:319-322.

Granett, J.; Retnakaran, A. 1977. Stadial susceptibility of eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), to the insect growth regulator Dimilin. Can. Entomol. 109:893-894.

Granett, J.; Robertson, J.; Retnakaran, A. 1980. Metabolic basis of differential susceptibility of two forest Lepidopterans to diflubenzuron. Entomol. exp. appl. 28:295-300.

Guan, X.C.; Wu, Z.X.; Wu, T.N.; Feng, H. 1978. Studies on rearing *Trichogramma dendrolimi* Matsumura *in vitro*. Acta. Entomol. Sin. 21:122-126 (Chinese, English Summary).

Hall, I.M. 1963. Microbial control. Pages 477-517 *in* E.A. Steinhaus, ed. Insect Pathology. An Advanced Treatise. Vol. 2. Academic Press, New York.

Harper, J.D. 1974. Forest insect control with *Bacillus thuringiensis*. Survey of current knowledge. Auburn University, Auburn, Alabama. 64 p.

Harvey, G.T.; Burke, J.M. 1974. Mortality of the spruce budworm on white spruce caused by *Entomophthora spaerosperma* Fresenius. Can. For. Serv., Ottawa, Bi-mon. Res. Notes 30:23-24.

Hodgkinson, R.S.; Finnis, M.; Shepherd, R.F.; Cunningham, J.C. 1979. Aerial application of nuclear polyhedrosis virus and *Bacillus thuringiensis* against western spruce budworm. B.C. Min. For./Can. For. Serv., Victoria, B.C. Joint Rep. No. 10. 19 p.

Hoffman, J.D.; Ignoffo, C.M.; Dickerson, W.A. 1975. *In vitro* rearing of the endoparasitic wasp, *Trichogramma pretiosum*. Ann. Entomol. Soc. Amer. 68:335-336.

House, H.L. 1967. The decreasing occurrence of diapause in the fly *Pseudosarcophaga affinis* through laboratory-reared generations. Can. J. Zool. 45:149-153.

Houseweart, M.W.; Southard, S.G.; Jennings, D.T. 1982. Availability and acceptibility of spruce budworm eggs to parasitism by the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). Can. Entomol. 114:657-666.

Houseweart, M.W., Jennings, D.T.; Welty, C.; Southard, S.G. 1983. Progeny production by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) utilizing eggs of *Choristoneura fumiferana* (Lepidoptera: Tortricidae) and *Sitotroga cerealella* (Lepidoptera: Gelechiidae). Can. Entomol. 115:1245-1252.

Houseweart, M.W.; Jennings, S.T.; Lawrence, R.K. 1984a. Field releases of *Trichogramma minutum* Riley for suppression of epidemic spruce budworm, *Choristoneura fumiferana* (Clemens), egg populations in Maine. Can. Entomol. 116:1345-1356.

Houseweart, M.W.; Jennings, D.T.; Pease, S.H.; Lawrence, R.K. 1984b. Alternate insect hosts and characteristics of forest stands supporting native populations of *Trichogramma minutum* Riley. Univ. of Maine, Cooperative Forest Research Unit, Res. Bull. 5. Maine Agric. Exp. Stn., Orono, ME. Misc. Rep. 300. 32 p.

Jennings, D.T.; Houseweart, M.W. 1983a. Parasitism of spruce budworm (Lepidoptera: Tortricidae) eggs by *Trichogramma minutum* and absence of overwintering parasitoids. Environ. Entomol. 12:535-540.

Jennings, D.T.; Houseweart, M.W. 1983b. Field attractiveness of (E)- and (Z)-11-tetradecenal pheromone blends to male spruce budworm moths, *Choristoneura fumiferana* (Clemens). J. Chem. Ecol. 9:1327-1332.

Kaya, H.K.; Reardon, R.C. 1982. Evaluation of *Neoaplectana carpocapsae* for biological control of the western spruce budworm, *Choristoneura occidentalis*: ineffectiveness and persistence of tank mixes. J. Nematol. 14:595-597.

Kaya, H.K.; Hara, A.H.; Reardon, R.C. 1981. Laboratory and field evaluation of *Neoaplectana carpocapsae* (Rhabdita: Steinernematidae) against the elm leaf beetle (Coleoptera: Chrysomelidae) and the western spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 113:787-793.

Kemp, W.P.; Simmons, G.A. 1978. The influence of stand factors on parasitism of spruce budworm eggs by *Trichogramma minutum*. Environ. Entomol. 7:685-688.

Klein, W.; Lewis, F. 1966. Experimental spraying with *Bacillus thuringiensis* for control of the spruce budworm. J. For. 64:458-462.

Klier, A.; Fargette, F.; Ribier, J.; Rapoport, G. 1982. Cloning and expression of the crystal protein genes from *Bacillus thuringiensis* strain berliner 1715. EMBO J. 1:791-799.

Kucera, D.R.; Taylor, R.G. 1984. Spruce budworms situation in North America in 1983. U.S. Dep. Agric., For. Serv., Washington, D.C. Misc. Publ. No. 1441. 27 p.

Kurtti, T.J.; Brooks, M.A. 1977. The rate of development of a microsporidian in moth cell culture. J. Invertebr. Pathol. 29:126-132.

LaChance, L.E. 1979. Genetic strategies affecting the success and economy of the sterile insect release method. Pages 8-18 *in* M.A. Hoy and J.J. McKilvry, eds. Genetics in Relation to Insect Management. Working Papers. Rockefeller Foundation.

Lawrence, R.K.; Houseweart, M.W.; Jennings, D.T.; Southard, S.G.; Halteman, W.A. 1985. Development rates of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) and implications for timing augmentative releases for suppression of egg populations of *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can.. Entomol. 117:557-563.

Leonard, D.R. 1975. Parasitization of the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) by *Brachymeria intermedia* (Nees) (Hymenoptera: Chalcididae). J. N.Y. Entomol. Soc. 83:269 (abst.).

Luthy, P.; Fischer, H.M.; Hutter, R. 1984. Deliberate release of microorganisms for insect control. Pages 55-64 *in* W. Arber, K. Iumensee, W.J. Peacock, and P. Starlinger, eds. Genetic manipulation: impact on man and society. Proc. 3rd Symp. Comm. on Genetic Exp. ICSU Press by Cambridge University Press.

Maas, W.; van Hes, R.; Grosscurt, A.C.; Deul, D.H. 1980. Benzoylphenylurea insecticides. Chem. Pflanzenschut. Schadl. 6:423-470.

MacVean, C.M.; Brewer, J.W.; Capinera, J.L. 1982. Field test of antidesiccants to extend the infection period of the entomogenous nematode *Neoaplectana carpocapsae* against the Colorado potato beetle. J. Econ. Entomol. 75:97-101.

Madore, C.D.; Boucias, D.G.; Dimond, J.B. 1983. Reduction of reproductive potential in spruce budworm (Lepidoptera: Tortricidae) by a chitin-inhibiting insect growth regulator. J. Econ. Entomol. 76:708-710.

McGugan, B.M.; Coppel, H.C. 1962. European spruce sawfly — *Diprion hercyniae* (Htg.) (Diprionidae). Pages 90-109 *in* A Review of the Biological Control Attempts Against Insects and Weeds in Canada. Part II. Biological Control of Forest Insects, 1910-1958. Commw. Inst. Biol. Control, Trinidad, Tech. Comm. No. 2. Commonw. Agric. Bureaux.

McGregor, M.D.; Hamel, D.R.; Lood, R.C. 1976. Dipel WP (*Bacillus thuringiensis* Berliner) as a control agent for western spruce budworm *Choristoneura occidentalis* Free. U.S. Dep. Agric., For. Serv. Northern Region, Missoula, MT. Rep. No. 76-11. 17 p.

Meighen, E.A.; Slessor, K.N.; Grant, G.G. 1981. A bioluminescent assay for aldehyde pheromones in insects. Experientia 37:555-556.

Meighen, E.A.; Slessor, K.N.; Grant, G.G. 1982. Development of a bioluminescence assay for aldehyde pheromones of insects. I. Sensitivity and specificity. J. Chem. Ecol. 8:911-921.

Meighen, E.A.; Szittner, R.B.; Grant, G.G. 1983. Determination of the release rate of aldehyde pheromones from insect lures by cold trapping and direct bioluminescence analysis. Anal. Biochem. 133:179-185.

Metalnikov, S.; Chorine, V. 1929. On the infection of the gypsy moth and certain other insects with *Bacterium thuringiensis*. A preliminary report. Sci. Rep. Int. Corn Borer Invest. 2:60-61.

Miller, C.A. 1953. Parasitism of spruce budworm eggs by *Trichogramma minutum*. Can. Dept. Agric., Sci. Serv., Div. of For. Biol., Ottawa. Bi-mon. Prog. Rep. 9(4):1.

Miller, C.A. 1963. Parasites of the spruce budworm. Pages 228-244 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Miller, C.A.; Otvos, I.S. 1981. Parasites and predators. Pages 133-134 *in* J. Hudak and A.G. Raske, eds. Review of the spruce budworm outbreak in Newfoundland — its control and forest management implications. Can. For. Serv. Submission to the Newfoundland and Labrador Royal Commission on Forest Protection and Management. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Inf. Rep. N-X-205.

Minot, M.C.; Leonard, D.E. 1976. Host preference and development of the parasitoid *Brachymeria intermedia* in *Lymantria dispar, Galleria mellonella* and *Choristoneura fumiferana*. Environ. Entomol. 5:527-532.

Morris, O.N. 1975. Susceptibility of the spruce budworm, *Choristoneura fumiferana*, and the white-marked tussock moth, *Orgyia leucostigma*, to *Bacillus thuringiensis*-chemical insecticide combinations. J. Invertebr. Pathol. 26:199-204.

Morris, O.N. 1976. A 2-year study of the efficacy of *Bacillus thuringiensis*-chitinase combinations in spruce budworm (*Choristoneura fumiferana*) control. Can. Entomol. 108:225-233.

Morris, O.N. 1977. Long term study of the effectiveness of aerial application of *Bacillus thuringiensis*-acephate combinations against the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 109:1239-1248.

Morris, O.N. 1980. Report on the 1979 CANUSA B.t. spray trials. Can. For. Serv., For. Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. FPM-X-40. 120 p.

Morris, O.N. 1981. Report on the 1980 Cooperative *Bacillus thuringiensis* (B.t.) spray trials. Can. For. Serv., For. Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. FPM-X-48. 75 p.

Morris, O.N. 1982a. Bacteria as pesticides: forest applications. Pages 239-287 *in* E. Kurstak, ed. Microbial and Viral Pesticides. Marcel Dekker, Inc., New York and Basel.

Morris, O.N. 1982b. Report of the 1981 Cooperative *Bacillus thuringiensis* (B.t.) spray trials. Can. For. Serv., For. Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. FPM-X-58. 87 p.

Morris, O.N. 1984a. Field response of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), to dosage and volume rates of commercial *Bacillus thuringiensis*. Can. Entomol. 116:983-990.

Morris, O.N. 1984b. Comparative efficacies of single and double applications of commercial *Bacillus thuringiensis* against the spruce budworm *Choristoneura fumiferana* in balsam fir stands. Can. Entomol. 116:101-102.

Morris, O.N.; Armstrong, J.A. 1975. Preliminary field trials with *Bacillus thuringiensis*-chemical insecticide combinations in the integrated control of the spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 107:1281-1288.

Morris, O.N.; Moore, A. 1983. Relative potencies of 50 isolates of *Bacillus thuringiensis* for larvae of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 115:815-822.

Morris, O.N.; Angus, T.A.; Smirnoff, W.A. 1975. Field trials of *Bacillus thuringiensis* against the spruce budworm, 1960-1973. Pages 129-133 *in* M.L. Prebble, ed. Aerial Control of Forest Insect Pests in Canada. Can. For. Serv., Ottawa, Ont.

Morris, O.N.; Hildebrand, M.J.; Armstrong, J.A. 1979. Preliminary field studies on the use of additives to improve deposition rate and efficacy of commercial formulations of *Bacillus thuringiensis* applied against the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. For. Serv., For. Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. FPM-X-32. 23 p.

Mott., D.G.; Angus, T.A.; Heimpel, A.M.; Fisher, R.A. 1961. Aerial spraying of Thuricide against the spruce budworm in New Brunswick. Can. Dept. For., For. Ent. and Path. Br., Ottawa. Bi-mon. Prog. Rep. 17(3):2.

Neilson, M.M. 1963. The analysis of egg survival in the unsprayed area. Pages 37-41 *in* R.F. Morris, ed. The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31.

Newsom, L.D. 1980. The next rung up the integrated pest management ladder. Bull. Entomol. Soc. Amer. 26:369-374.

Otvos, I.S.; Moody, B.H. 1978. The spruce budworm in Newfoundland: history, status and control. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Inf. Rep. N-X-150. 76 p.

Outram, I. 1975. Field trials of insect growth regulators against the spruce budworm, New Brunswick, 1973. Pages 143-146 *in* M.L. Prebble, ed. Aerial control of forest insects in Canada. Can. For. Serv., Ottawa, Ont.

Palaniswamy, P.; Ross, R.J.; Seabrook, W.D.; Lonergan, G.C.; Weisner, C.J.; Tan, S.H.; Silk, P.J. 1982. Mating suppression of caged spruce budworm (Lepidoptera: Tortricidae) moths in different pheromone atmospheres and high population densities. J. Econ. Entomol. 75:989-993.

Percy, J.; Fast, P.G. 1983. *Bacillus thuringiensis* crystal toxin: ultrastructural studies of its effect on silkworm midgut cells. J. Invertebr. Pathol. 41:86-98.

Perry, D.F.; Tyrrell, D.; DeLyzer, A.J. 1982a. The mode of germination of *Zoophthora radicans* zygospores. Mycologia 74:549-554.

Perry, D.F.; Latteur, G.; Wilding, N. 1982b. The environmental persistence of propagules of the Entomophthorales. Pages 325-329 *in* Proc. 3rd Int. Coll. Invertebr. Pathol. and 15th Annu. Meet. Soc. Invertebr. Pathol., Brighton, UK. Sept. 1982.

Perry, D.F.; Whitfield, G.H. 1984. The interrelationships between microbial entomopathogens and insect hosts: a system study approach with particular reference to the entomophthorales and the eastern spruce budworm. Pages 307-331 *in* J.M. Anderson, A.D.M. Rayner and D.W.H. Walton, eds. Proc. Joint Brit. Mycol. Soc. Brit. Ecol. Soc. Meet. Exeter, UK. Sept. 1982.

Quinstad, G.B.; Cerf, D.C.; Schooley, D.A.; Staal, G.B. 1981. Fluoromevalonate acts as an inhibitor of insect juvenile hormone biosynthesis. Nature 289:176-177.

Ragenovich, I.R. 1983. Pilot project to evaluate the operational use of *Bacillus thuringiensis* against the western spruce budworm in northern New Mexico, 1981-82. Prog. Rep. No. 1. U.S. Dep. Agric., For. Serv., S.W. Region, Albuquerque, NM. R-3 84-1. 62 p.

Rappaport, N.G.; Robertson, J.L. 1981. Lethal effects of five molt inhibitors fed to the western spruce budworm (*Choristoneura occidentalis* Freeman) (Lepidoptera: Tortricidae) and the Douglas-fir tussock moth (*Orgyia pseudotsugata* [McDonnough]) (Lepidoptera: Lymantriidae). Z. Angew. Entomol. 91:459-463.

Reardon, R.C.; Johnson, D.R.; Narog, M.G.; Banadi, S.E.; Hubbard, H.B., Jr. 1982. Efficacy of two formulations of *Bacillus thuringiensis*, Thuricide 16B and Dipel 4L, on populations of spruce budworm on balsam fir in Wisconsin. J. Econ. Entomol. 75:509-514.

Retnakaran, A. 1970. Preliminary results of radiation induced sterility of the male spruce budworm. Can. For. Serv., Ottawa. Bi-mon. Res. Notes 26:13-14.

Retnakaran, A. 1971. Thiotepa as an effective agent for mass sterilizing the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 103:1753-1756.

Retnakaran, A. 1980. Effect of three new moult-inhibiting insect growth regulators on the spruce budworm. J. Econ. Entomol. 73:520-524.

Retnakaran, A. 1981. Toxicology and efficacy of insect growth regulators aerially applied against the spruce budworm at Hearst (1978), Wawa (1979) and the French River area (1980). Can. For. Serv., For. Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. FPM-X-45. 63 p.

Retnakaran, A. 1982. Laboratory and field evaluation of a fast-acting insect growth regulator against the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 114:523-530.

Retnakaran, A. 1983. Spectrophotometric determination of larval ingestion rates in the spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 115:31-40.

Retnakaran, A.; Smith, L. 1975. Morphogenetic effects of an inhibitor of cuticle development on the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 107:883-886.

Retnakaran, A.; Howse, G.M.; Kaupp, W. 1977. Experimental aerial application of insect growth regulators against the spruce budworm *Choristoneura fumiferana* (Clem.) in Manitoulin Island in 1974 and 1975. Can. For. Serv., For. Pest. Manage. Inst., Sault Ste. Marie, Inf. Rep. IP-X-13. 32 p.

Retnakaran, A.; Kaupp, W.; Howse, G. 1978. Experimental aerial application of insect growth regulators against the spruce budworm in Thessalon (1976) and Hearst (1977). Can. For. Serv., For. Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. FPM-X-19. 29 p.

Retnakaran, A.; Granett, J.; Robertson, J. 1980. Possible physiological mechanisms for the differential susceptibility of two forest lepidoptera to diflubenzuron. J. Insect Physiol. 26:385-390.

Retnakaran, A.; Grant, G.G.; Ennis, T.J.; Fast, P.G.; Arif, B.M.; Tyrrell, D.; Wilson, G. 1982. Development of environmentally acceptable methods of controlling insect pests in forests. Can. For. Serv., For. Pest Manage. Inst. Sault Ste. Marie, Inf. Rep. FPM-X-62. 22 p.

Retnakaran, A.; Granett, J.; Ennis, T.J. 1985. Insect Growth Regulators. Pages 529-601 *in* G.A. Kerkut and L.I. Gilbert eds. Comprehensive Insect Physiology, Biochemistry and Pharmacology. Vol. 12. Pergamon Press, Great Britain.

Ridgway, R.L.; Ables, J.R.; Goodpasture, C.; Hartstack, A.W. 1981. *Trichogramma* and its utilization for crop protection in the USA. Pages 41-48 *in* J.R. Coulson, ed. Proc. Joint American-Soviet Conf. on use of beneficial organisms in the control of crop pests. Washington, D.C. Aug. 1979. Entomol. Soc. Amer. Publ.

Robertson, J.L. 1982. Toxicity of experimental molt inhibitors to western spruce budworm. J. Ga. Entomol. Soc. 17:413-416.

Robertson, J.L.; Kimball, R.A. 1979a. Effects of insect growth regulators on the western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae). I. Lethal effects of last instar treatments. Can. Entomol. 111:1361-1368.

Robertson, J.L.; Kimball, R.A. 1979b. Effects of insect growth regulators on the western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae). II. Fecundity and fertility reduction following last instar treatments. Can. Entomol. 111:1369-1380.

Robertson, J.L.; Haverty, M.I. 1981. Multiphase laboratory bioassays to select chemicals for field-testing on the western spruce budworm. J. Econ. Entomol. 74:148-153.

Robertson, J.L.; Kimball, R.A. 1981. Variables affecting the practical use of juvenile hormone analogues for control of the western spruce budworm (*Choristoneura occidentalis*) (Lepidoptera: Tortricidae). Can. Entomol. 113:827-844.

Robertson, J.L.; Haverty, M.I. 1982. Estimation of rates and times of application for selected insect growth regulator formulations applied to western spruce budworm. J. Ga. Entomol. Soc. 17:297-307.

Ross, R.J.; Seabrook, W.D.; Lonergan, G.C.; Paniswamy, P.; Ponder, B. 1982. Effect of blends of sex pheromone isomers in mating and electroantennograms of spruce budworm (Lepidoptera: Tortricidae). Can. Entomol. 114:1143-1149.

Sanders, C.J. 1976. Disruption of sex attraction in the eastern spruce budworm. Environ. Entomol. 5:868-872.

Sanders, C.J. 1978. Evaluation of sex attractant traps for monitoring spruce budworm populations (Lepidoptera: Tortricidae). Can. Entomol. 110:43-50.

Sanders, C.J. 1979a. Mate location and mating in eastern spruce budworm. Can. For. Serv., Ottawa. Bimon. Res. Notes 35:2-3.

Sanders, C.J. 1979b. Spruce budworm mating disruption trials using synthetic attractant in Conrel fibres (Ontario, 1977). Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Inf. Rep. O-X-285. 32 p.

Sanders, C.J., (Compiler). 1980. A summary of current techniques used for sampling spruce budworm populations and estimating defoliation in eastern Canada. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Inf. Rep. O-X-306. 33 p.

Sanders, C.J. 1981. Spruce budworm: effects of different blends of sex pheromone components on disruption of male attraction. Experientia 37:1176-1178.

Sanders, C.J. 1982. Disruption of male spruce budworm orientation to calling females in a wind tunnel with synthetic pheromone. J. Chem. Ecol. 8:493-506.

Sanders, C.J. 1984. Sex pheromone of the spruce budworm (Lepidoptera: Tortricidae): evidence for a missing component. Can. Entomol. 116:93-100.

Sanders, C.J.; Weatherston, J. 1976. Sex pheromone of the eastern spruce budworm (Lepidoptera: Tortricidae): Optimum blend of *trans*- and *cis*-11-tetradecenal. Can. Entomol. 108:1285-1290.

Sanders, C.J.; Seabrook, W.D. 1982. Disruption of mating in the spruce budworm, *Choristoneura fumiferana* (Clemens). Pages 175-183 *in* A.F. Kydonieus and M. Beroza, eds. Insect Suppression with Controlled Release Pheromone Systems. Vol. 2. CRC Press.

Sanders, C.J.; Silk, P.J. 1982. Disruption of spruce budworm mating by means of Hercon plastic laminated flakes, Ontario 1981. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Inf. Rep. O-X-335. 22 p.

Schmiege, D.C. 1963. The feasibility of using a neoaplectanid nematode for control of some forest insect pests. J. Econ. Entomol. 56:427-431.

Schmidt, J.O.; Seabrook, W.D. 1979. Mating of caged spruce budworm moths in pheromone environments. J. Econ. Entomol. 72:509-511.

Schmidt, J.O.; Thomas, A.W.; Seabrook, W.D. 1980. Mating of caged moths in forests treated with a Conrel hollow-fibre pheromone formulation. Can. For. Serv., Ottawa. Bi-mon. Res. Notes 36:25.

Schnepf, H.E.; Whiteley, H.R. 1981. Cloning and expression of the *Bacillus thuringiensis* crystal protein gene in *Escherichia coli*. Proc. Natl. Acad. Sci. USA 78:2893-2897.

Shapiro, M.; Martignoni, M.E.; Cunningham, J.C.; Goodwin, R.H. 1982. Potential use of the saltmarsh caterpillar as a production host for nucleopolyhedrosis viruses. J. Econ. Entomol. 75:69-71.

Shepherd, R.F.; Gray, T.G.; Cunningham, J.C. 1982. Effects of nuclear polyhedrosis virus and *Bacillus thuringiensis* on western spruce budworm (Lepidoptera: Tortricidae) 1 and 2 years after aerial application. Can. Entomol. 114: 281-282.

Silk, P.J.; Kuenen, L.P.S. 1984. Sex pheromones and their potential as control agents for forest lepidoptera in eastern Canada. Pages 35-47 *in* Implication of chemical and biological control agents in forestry applications. Amer. Chem. Soc., Washington, D.C. Symposium Series.

Silk, P.J.; Tan, S.H.; Wiesner, C.J.; Ross, R.J.; Lonergan, G.C. 1980. Sex pheromone chemistry of the eastern spruce budworm, *Choristoneura fumiferana*. Environ. Entomol. 9:640-644.

Silk, P.J.; Weisner, C.J.; Tan, S.H.; Ross, R.J.; Grant, G.G. 1982. Sex pheromone chemistry of the western spruce budworm, *Choristoneura occidentalis* Free. J. Chem. Ecol. 8:351-362.

Smirnoff, W.A. 1963. Tests of *Bacillus thuringiensis* var. *thuringiensis* Berliner and *B. cereus* Frankland and Frankland on larvae of *Choristoneura fumiferana* Clemens. Can. Entomol. 95:127-133.

Smirnoff, W.A. 1971. Effect of chitinase on the action of *Bacillus thuringiensis*. Can. Entomol. 103:1829-1831.

Smirnoff, W.A. 1973. Results of tests with *Bacillus thuringiensis* and chitinase on larvae of the spruce budworm. J. Invertebr. Pathol. 21:116-118.

Smirnoff, W.A. 1974a. The symptoms of infection by *Bacillus thuringiensis*-chitinase formulation in larvae of *Choristoneura fumiferana*. J. Invertebr. Pathol. 23:397-399.

Smirnoff, W.A. 1974b. Three years of aerial field experiments with *Bacillus thuringiensis* plus chitinase formulation against the spruce budworm. J. Invertebr. Pathol. 24:344-348.

Smirnoff, W.A. 1985. Field tests with a highly concentrated *Bacillus thuringiensis* formula against spruce budworm *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *In* D.G. Grimble and F.B. Lewis, tech. coords. Proc. Symp. Microbial Control of Spruce Budworms and Gypsy Moths. 10-12 April 1984, Windsor Locks, CT. U.S. Dep. Agric. For. Serv., Broomall, PA. Gen. Tech. Rep. NE-100, 175 p.

Smirnoff, W.A.; Valero, J.R. 1983. Characteristics of a highly concentrated *Bacillus thuringiensis* formulation against spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 115:443-444.

Smirnoff, W.A.; Juneau, A.; Valero, J. 1972. Results of experimental aerial spraying of *Bacillus thuringiensis* against spruce budworm larvae. Can. For. Serv., Ottawa. Bi-mon. Res. Notes 28:1-2.

Smirnoff, W.A.; Larsen, L.V.; Juneau, A.; Valero, J. 1974. Test with a highly concentrated low-volume formulation of *Bacillus thuringiensis* against spruce budworm. Can. For. Serv., Ottawa. Bi-mon. Res. Notes 30:9.

Smirnoff, W.A.; Juneau, A.; Valero, J.R. 1982. Essai d'une préparation ultra-concentrée de *Bacillus thuringiensis* conte la tordeuse des bourgeons de l'épinette. Can. J. Forest. Res. 12:105-107.

Sohi, S.S.; Wilson, G.G. 1976. Persistent infection of *Malacosoma disstria* (Lepidoptera: Lasiocampidae) cell cultures with *Nosema (Glugea) disstriae* (Microsporidia: Nosematidae). Can. J. Zool. 54:336-342.

Soper, R.S. 1985. *Erynia radicans*: potential mycoinsecticide for spruce budworm control. *In* D.G. Grimble and F.B. Lewis, tech. coords. Proc. Symp. Microbial Control of Spruce Budworms and Gypsy Moths. 10-12 April 1984, Windsor Locks, CT. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-100. 175 p.

Southard, S.G.; Houseweart, M.W.; Jennings, D.T.; Halteman, W.A. 1982. Size differences of laboratory reared and wild populations of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). Can. Entomol. 114:693-698.

Stairs, G.R.; Bird, F.T. 1962. Dissemination of viruses against the spruce budworm, *Choristoneura fumiferana* (Clemens). Can. Entomol. 94:966-969.

Stairs, G.R.; Fraser, T.; Fraser, M. 1981. Changes in growth and virulence of a nuclear polyhedrosis virus from *Choristoneura fumiferana* after passage in *Trichoplusia ni* and *Galleria mellonella*. J. Invertebr. Pathol. 38:230-235.

Strunz, G.M.; Fogal, W.H. 1981. Antifeedants. Pages 136-137 *in* J. Hudak and A.G. Raske, eds. Review of the spruce budworm outbreak in Newfoundland — its control and forest management implications. Can. For. Serv. Submission to the Newfoundland and Labrador Royal Commission on Forest Protection and Management. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Inf. Rep. N-X-205.

Szittner, R.B.; Morse, D.; Grant, G.G.; Meighen, E.A. 1982. Development of a bioluminescence assay for aldehyde pheromones of insects. III. Analysis of airborne pheromone. J. Chem. Ecol. 8:935-945.

Thomas, H.A. 1966. Parasitism by *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) in the spruce budworm outbreak in Maine. Ann. Entomol. Soc. Amer. 59:723-725.

Thomson, H.M. 1958. The effect of a microsporidian parasite on the development, reproduction and mortality of the spruce budworm *Choristoneura fumiferana* (Clem.). Can. J. Zool. 36:499-511.

Thompson, C.G.; Neisess, J.; Batzer, H.O. 1977. Field tests of *Bacillus thuringiensis* and aerial application strategies on western mountainous terrain. U.S. Dep. Agric., For. Serv., Pac. Northwest For. Exp. Stn., Portland, OR. Res. Pap. PNW-230. 12 p.

Tripp, H.A. 1972. Field trials to control spruce budworm, *Choristoneura fumiferana* (Clem.), through aerial application of *Bacillus thuringiensis*. Proc. Entomol. Soc. Ont. 103:64-69.

Tyrrell, D. 1981. Fungi. Pages 132-133 *in* J. Hudak and A.G. Raske, eds. Review of the spruce budworm outbreak in Newfoundland — its control and forest management implications. Can. For. Serv. Submission to the Newfoundland and Labrador Royal Commission on Forest Protection and Management. Can. For. Serv., Nfld. For. Res. Cent., St. John's, Inf. Rep. N-X-205.

Tyrrell, D.; MacLeod, D.M. 1972. Spontaneous formation of protoplasts by a species of *Entomophthora*. J. Invertebr. Pathol. 19:354-360.

Valli, V.E.; Cunningham, J.C.; Arif, B.M. 1976. Tests demonstrating the safety of a baculovirus of the spruce budworm to mammals and birds. Pages 445-446 *in* Proc. 1st Internat. Coll. Invertebr. Pathol. and 9th Annu. Meet. Soc. Invertebr. Pathol., Queen's University, Kingston, Canada.

Vandenberg, J.D.; Soper, R.S. 1975. Prevalence of Entomophthorales mycoses in populations of spruce budworm, *Choristoneura fumiferana*. Environ. Entomol. 7:847-853.

van Roermund, H.J.W.; Perry, D.F.; Tyrrell, D. 1984. Influence of temperature, light, nutrients and pH in determination of the mode of conidial germination in *Zoophthora radicans*. Trans. Brit. Mycol. Soc. 82:31-38.

Varty, I.W. 1984. Parasitoids of the spruce budworm. Pages 267-272 *in* J.S. Kelleher and M.A. Hulme, eds. Biological control of insects and weeds in Canada, 1969-1980. Commonw. Agric. Bureaux, Slough, England.

Walton, G.S.; Lewis, F.B. 1982. Spruce budworm core B.t. test — 1980 combined summary. U.S. Dep. Agric. For. Serv. N.E. For. Exp. Station. Orono, ME. Res. Pap. NE-506. 12 p.

Weatherston, J.; Roelofs, W.; Comeau, A.; Sanders, C.J. 1971. Studies of physiologically active arthropod secretions. X. Sex pheromone of the eastern spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 103:1741-1747.

Weisner, C.J.; Silk, P.J. 1982. Monitoring the performance of eastern spruce budworm pheromone formulations. Pages 209-217 *in* B.A. Leonhardt and M. Beroza, eds. Insect Pheromone Technology: Chemistry and Applications. Amer. Chem. Soc. Symp. Ser. No. 190.

Weisner, C.J.; Silk, P.J.; Tan, S.H.; Fullarton, S. 1980. Monitoring of atmospheric concentrations of the sex pheromone of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 112:333-334.

Wilcox, H., III.; Coffey, T., Jr., (Compilers). 1978. Environmental impacts of diflubenzuron (Dimilin®) insecticide. Forest Insect and Disease Management, U.S. Dep. Agric., For. Serv. Broomall, PA. 18 p.

Wilson, G.G. 1977. The effects of feeding microsporidian (*Nosema fumiferanae*) spores to naturally infected spruce budworm (*Choristoneura fumiferana*). Can. J. Zool. 55:249-250.

Wilson, G.G. 1978. Microsporidian infection in spruce budworm (*Choristoneura fumiferana*) 1 and 2 years after application. Can. For. Serv., Ottawa. Bi-mon. Res. Notes 34:16.

Wilson, G.G. 1981. *Nosema fumiferanae*, a natural pathogen of a forest pest: potential for pest management. Pages 595-601 *in* H.D. Burges, ed. Microbial Control of Pests and Plant Diseases 1970-1980. Academic Press, London.

Wilson, G.G. 1982a. Protozoans for insect control. Pages 587-600 *in* E. Kurstak, ed. Microbial and Viral Pesticides. Marcel Dekker Inc., New York and Basel.

Wilson, G.G. 1982b. Transmission of *Nosema fumiferanae* (Microsporidia) to its host *Choristoneura fumiferana* (Clem.). Z. Parasitenkd. 68:47-51.

Wilson, G.G.; Kaupp, W.J. 1975. Application of a microsporidia, *Nosema fumiferanae*, against spruce budworm on Manitoulin Island, 1975. Can. For. Serv., For. Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. IP-X-11. 26 p.

Wilson, G.G.; Kaupp, W.J. 1976a. Application of *Nosema fumiferanae* and *Pleistophora schubergi* (Microsporidia) against the spruce budworm in Ontario, 1976. Can. For. Serv., For. Pest Manage. Inst., Sault Ste. Marie, Inf. Rep. IP-X-15. 14 p.

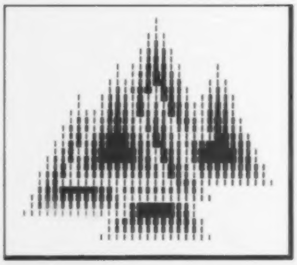
Wilson, G.G.; Kaupp, W.J. 1976b. Incidence of *Nosema fumiferanae* in spruce budworm, *Choristoneura fumiferana* in the year following application. Can. For. Serv., Ottawa. Bi-mon. Res. Notes 32:32.

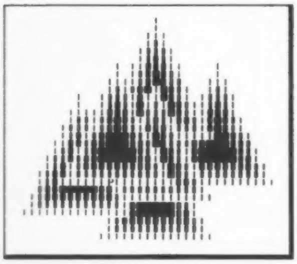
Wong, H.C.; Schnepf, H.E.; Whiteley, H.R. 1983. Transcription and translational start sites for *Bacillus thuringiensis* crystal protein gene. J. Biol. Chem. 258:1960-1967.

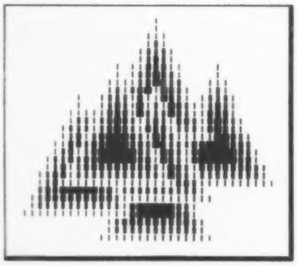
Wu, Z.X.; Zhang, Z.P.; Li, T.X.; Liv, D.M. 1980. Artificial media devoid of insect additives for rearing larvae of the endoparasitoid wasp, *Trichogramma*. Acta. Entomol. Sin. 23:232 (Chinese).

Workshop III — Forest Stands and Budworms

How do stand types differ in susceptibility and vulnerability and what are the implications for forest management?







Workshop III — Forest Stands and Budworms

Moderator: ***W.C. Schmidt***

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For too long, silviculturists and entomologists have not talked a common language. As a result, silvicultural prescriptions have often been implemented that do not adequately consider the impact these silvicultural operations may have on the insect complex. The reverse equation is also true — entomologists have given less than adequate consideration to the forest that provides the substrate for the budworm and thus, perpetuate the budworm problem. It is only when these two disciplines begin to interact in developing prescriptions for budworm host forests that we can expect realistic forest management practices that will reduce budworm problems in both Eastern and Western North America. A fundamental question is — do we manage the forest or the budworm? The emphasis in this workshop is on the forest.

This workshop — appropriately labeled forest stands and budworms — asks the question, "How do stand types differ in susceptibility and vulnerability and what are the implications for forest management?" The first section of this workship describes the characteristics of susceptible/vulnerable stands and how these terms are often interpreted. Emphasis is on the stand, as opposed to broad expanses of host forests. This permits inclusion of stand conditions, such as age, density, site productivity, species composition, stage of succession, elevation, juxtaposition, and others appropriate for specific stands.

The second section of this workshop describes different hazard rating systems that are developed, or being developed, for evaluating host stands on both eastern and western forests of this continent. Information of this type permits prioritizing of pest management practices appropriate for a given forest management unit.

The third section of this workshop discusses silvicultural strategies to reduce susceptibility/vulnerability of budworm host forests. The similar, yet different, host forests of the East and West present a challenging array of conditions that must be dealt with in developing silvicultural prescriptions appropriate for a particular stand and site condition. However, silviculture principles do have commonalities based on ecological facts of the eastern and western ecosystems. By its very nature, silviculture is an integrative science that must consider a broad array of conditions — one of which is the budworm situation — as well as the overall management objectives for a particular unit of land. This section focuses mostly on those forests where silviculture can be practiced, as opposed to wilderness

Pendant trop longtemps, les sylviculteurs et les entomologistes n'ont pas parlé le même langage, avec, comme résultat, que souvent les possibilités prescrites par les premiers ne tenaient pas suffisamment compte du complexe des insectes. L'inverse est également vrai: les entomologistes ayant négligé le fait que la forêt constitue le milieu dont se nourrit la tordeuse et qu'elle perpétue le problème que cet insecte cause. Ce n'est que lorsque ces deux professions commenceront à dialoguer, pour prescrire la possibilité des forêts hôtes, que nous pourrons nous attendre à un aménagement rationnel qui corrigera le problème dans l'est et dans l'ouest de l'Amérique du Nord. Une question fondamentale à laquelle il faut répondre est celle-ci: «Faut-il aménager la forêt ou juguler la tordeuse?» Le présent atelier insiste sur l'aménagement.

Portant à juste titre sur les peuplements et les tordeuses, cet atelier a pour objet de répondre à la question suivante:

«Quelles sont les différences de vulnérabilité et de susceptibilité (possibilité d'infestation) entre les peuplements et quelles en sont les conséquences pour l'aménagement?» Durant la première partie de l'atelier, nous décrirons les caractéristiques de ces peuplements ainsi que les acceptions courantes de la susceptibilité et de la vulnérabilité. Nous insisterons sur le peuplement, par opposition aux vastes massifs hôtes, ce qui permet de tenir compte de l'âge, de la densité, de la productivité des stations, de la composition des espèces, du stade de la succession, de l'altitude, de la juxtaposition et d'autres conditions appropriées à des peuplements particuliers.

La deuxième partie portera sur les différents systèmes, actuels ou proposés, d'évaluation des risques pour les peuplements de l'est et de l'ouest de notre continent et qui permettent d'adopter pour la lutte contre les ravageurs un ordre de priorités qui convient à une unité donnée d'aménagement forestier.

La troisième partie de l'atelier portera sur les stratégies sylvicoles visant à réduire la susceptibilité et la vulnérabilité aux tordeuses. Dans l'Est et l'Ouest, les forêts semblables, tout en étant différentes, présentent un ensemble de conditions qui constituent un défi quand il s'agit de prescrire la possibilité de chaque peuplement et station. Cependant, les principes de la sylviculture partagent des caractéristiques communes, fondées sur des faits écologiques propres aux écosystèmes de l'Est et de l'Ouest. Intrinsèquement, la sylviculture est une science intégratrice qui doit tenir

and park areas where stands generally are not manipulated. In general, silviculture will be practiced, with or without the budworm, over vast areas of the East and West. It is particularly important that these silvicultural practices be designed to reduce susceptibility and vulnerability of the forest to the budworm, setting in motion both a short- and a long-term solution to what has been a long-term problem.

Drs. Witter, Fellin, and Stoszek, respectively, lead the discussions for the three sections — Characteristics of Susceptible/Vulnerable Stands, Hazard Rating, and Silvicultural Strategies — that follows, and I thank them for their contribution to this important topic.

compte d'une large gamme de conditions, dont l'une est la situation de la tordeuse, de même que des objectifs d'aménagement de l'ensemble d'une unité donnée du territoire. Cette partie de l'atelier portera surtout sur les forêts qu'on peut assujettir à la sylviculture, par opposition aux régions sauvages et aux parcs où les peuplements sont généralement laissés dans leur état. En général, la sylviculture portera, en l'absence ou non de tordeuse, sur de vastes superficies de l'Est et de l'Ouest. Il importe particulièrement que ses méthodes soient conçues pour réduire la susceptibilité et la vulnérabilité aux tordeuses, en mettant en place une solution à court et à long terme pour ce problème de longue date.

MM. Witter, Fellin et Stoszek animeront respectivement les trois parties de l'atelier (caractéristiques des peuplements susceptibles et vulnérables; évaluation des risques; stratégies sylvicoles). Je les remercie pour leur contribution à cette question importante.

Characteristics of Susceptible/ Vulnerable Stands

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This is a concise report of the key points discussed in this session by our panel or by participating members of the workshop. Panel members were: Robert Frank (USDA Forest Service, Orono, Maine), David MacLean (Maritimes Forest Research Centre, Fredericton, N.B.), Marcia McKeague (Great Northern Paper Company, Millinocket, Maine), Art Raske (Newfoundland Forest Research Centre, St. John's, Nfld.) and Karl Stoszek (University of Idaho, Moscow, Id.). No formal papers were presented at this session because most panel members had presented papers on related topics in other sessions.

Four terms are often used when discussing the effects of budworms on forest stands:

Susceptibility — likelihood that a stand will be attacked by the budworm.

Risk-rating system — a ranking of forest stands according to their susceptibility to the spruce budworm.

Vulnerability — likelihood of damage to the stand once budworm attack occurs.

Hazard-rating system — a ranking of forest stands according to their vulnerability to the spruce budworm.

These concepts are interrelated insofar as susceptibility determines the severity of attack and hence the level of damage to occur. Vulnerability also may be affected by factors other than stand characteristics such as individual tree condition. Most rating systems currently being used in North America rate the vulnerability of a stand.

Any spruce-fir stand or host tree in eastern North America is susceptible to attack by the spruce budworm. As a general rule, certain factors increase the amount of volume loss and tree mortality from spruce budworm outbreaks. Stand mortality usually increases with the severity and length of the outbreak. Stands with large balsam fir components have greater potential for mortality than stands comprised mostly of spruce and hardwoods. In general, mortality in mature fir stands ranges from 70 to 100 percent, whereas mortality in immature stands varies from 30 to 70 percent (MacLean 1980). Mortality of fir and spruce increases as their density increases within the stand. Spruce and balsam fir in two-storied stands under hardwood cover are less exposed to damage from the spruce budworm. Open stands in which spike tops of host species protrude from the forest canopy may suffer more damage. Stands on abnormally dry or wet sites usually sustain more damage. Damage often increases as the continuity and size of the host stand increases. Stands located downwind of a current outbreak are more likely to be infested, and stands located at elevations lower than 700 m (2,300 ft) and at latitudes south of 50° latitude are more likely to be damaged.

The impact of the western spruce budworm on susceptible stands varies considerably depending upon the species composition, stand density, stand age, and site characteristics. Dense, mature, pure stands of host species are highly prone to damage. Defoliation increases in Douglas-fir stands as crown closure increases. Stands composed of mixed species are less vulnerable than pure stands of host species. Volume loss is greater in shade-tolerant than in shade-intolerant species. The western spruce budworm does not appear to be a problem in young managed stands under 20 years of age. Growth loss is highest in dry Douglas-fir habitat types at low elevations on steep slopes, whereas cooler, wetter habitats sustain less injury. Also, more defoliation of Douglas-fir occurs on sites with shallow and dry soils.

Wulf and Carlson (in press) recently developed a method for rating the relative susceptibility of forest stands to the western spruce budworm. The model appears applicable to conifer stands over most of the northern U.S. Rocky Mountains. Index values are assigned to classes of each variable and multiplied over all factors for a given stand to determine the stand-susceptibility index for a given stand. The susceptibility index is based on the following variables: percent host crown cover, percent crown cover of all species, relative stand density, mean host age, coefficient of variation of height structure, habitat type, National Forest, and percent host type in surrounding forest (Carlson et al. in press). This interpretive model currently serves as a good working hypothesis for western spruce budworm dynamics.

The following two questions were discussed in detail:

1. From your point of view, briefly discuss one important research contribution relating to susceptible and vulnerable stands that were made during the CANUSA Program.
2. What are the important questions that should be addressed during the next 10 years relating to research in the area of susceptible and vulnerable stands?

Numerous contributions relating to better understanding of the budworm/host interactions have been made during the last 7 years. For more detailed information, see Carlson et al. (in press), Ostaff et al. 1984, Talerico and Montgomery 1983, USDA 1985, Witter et al. 1984, Witter and Lynch 1985, Wulf and Carlson (in press), Wulf and Cates (in press). The major contributions discussed in the workshop were: 1) better understanding of the effect of food quality on budworm survival; 2) better understanding of the relationship between the site, the stand, and budworm impact; 3) better quantification of budworm impact under various stand conditions; 4) better sampling methodology for measuring impact; 5) development of vulnerability indexes for New Brunswick, Nova Scotia, and Quebec; 6) development of a method to forecast wood production in stands defoliated by the spruce budworm; 7) development of hazard models for the western spruce budworm and for the spruce budworm in the Lake States; and 8) development of the Prognosis Model and Western Budworm Model so that users will be able to simulate the effects of intermediate treatments in various types of stands on western spruce budworm populations.

There were numerous discussions on what questions should be addressed during the next 10 years. Some of the key factors discussed were:

1. It is important for research scientists to continue detailed work on the effect of foliage quality on budworm survival. And it is time to study the applied aspects of this relationship such as budworm survival under different stand and site conditions.
2. Increased emphasis on development of ecological site classification systems for budworm susceptible stands is needed. We will be able to really understand the complex interactions between the budworm and the host only when we can compare tree mortality by site units, age class, soil types, physiography, site class, etc.
3. Continued research emphasis needs to be placed on the relationships and interactions between insect population densities, stand and site conditions, and impact.
4. Factors affecting tree vigor and tree stress need to be better understood. Entomologists must study the effects of multiple interactions (i.e., moisture relationships, insects, diseases, acid deposition) on tree and stand growth and survival.
5. Volume growth loss information should be included in future hazard-rating systems developed for eastern North America.
6. The currently developed systems fail to consider the effects of protection of the stand, by using chemical or microbial insecticides, on growth loss and stand mortality.
7. Additional information is needed on the effects of spruce budworm defoliation on white and red spruce.

Literature Cited

Carlson, C.E.; Schmidt, W.C.; Wulf, N.W. (In press). Silvicultural treatment. *In* Chapter 7, M.H. Brookes, J.J. Colbert, R.G. Mitchell and R.W. Stark, tech. coords. Managing trees and stands susceptible to western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1695.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56: 213-221.

Ostaff, D.P.; Cameron, M.D.; Mullins, E.J., assoc. eds. 1984. Proceedings of the Damage Assessment Working Group CANUSA Spruce Budworms Program 25-26 October 1983. Bangor, Maine. Canadian Forestry Service, Ottawa, Ont.

Talerico, R.L.; Montgomery, M.E., eds. 1983. Proceedings, forest defoliator-host interactions: a comparison between gypsy moth and spruce budworms. CANUSA workshop, 5-7 April 1983, New Haven, CT. U.S. Dep. Agric., For. Serv. Northeastern Sta., Broomall, PA. Gen. Tech. Rep. NE-85.

USDA Forest Service. 1985. Spruce-fir management and spruce budworm. Society of American Foresters Region VI Technical Conference 24-26 April 1984, Burlington, Vt. U.S. Dep. Agric., For. Serv. Northeastern Sta., Broomall, PA. Gen. Tech Rep. NE-99.

Witter, J.A.; Lynch, A.M. 1985. Rating spruce-fir stands for spruce budworm damage in Eastern North America. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 636.

Witter, J.; Ostaff, D.; Montgomery, B. 1984. Damage assessment. *In* Chapter 4, D.M. Schmitt, D.G. Grimble, and J.L. Searcy, tech. coords. Managing the spruce budworm in eastern North America. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 620.

Wulf, N.W., Carlson, C.E. (In press). Rating stand hazard to western spruce budworm. *In* Chapter 6, M.H. Brookes, R.W. Stark, R.G. Mitchell, and J.J. Colbert, tech. coords. Managing trees and stands susceptible to western spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Tech. Bull. 1695.

Wulf, N.W.; Cates, R.G. (In press). Site and stand characteristics related to budworm density and tree damage. Chapter 7 *in* M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark, tech. coords. Western spruce budworm. U.S. Dept. Agric., For. Serv., Washington, D.C. Tech. Bull. 1694.

Discussion Group B —
Hazard Rating

Vulnerability of Newfoundland Forests to Spruce Budworm Damage

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A forest rating for vulnerability to a given pest obviously depends on a consistent relation between forest type, measured by one or more parameters, and degree of pest damage. Such a clear relation was largely absent for damage to Newfoundland forests caused by the spruce budworm during the outbreak in the 1970s.

Some past studies on vulnerability to budworm may have been based on samples too small to detect differences, but this study used practically all the productive forests of the Province in 1-ha (2.5-acre) units.

Its major conclusion, however, does not differ much from the conclusions of earlier investigators. MacLean (1980) summarized vulnerability studies: "Prediction of the total expected mortality in a given stand is more difficult, however, and attempts to relate mortality to stand characteristics have not shown strong relationships." In later studies, however, MacLean (1982) and Blais and Archambault (1982) applied a vulnerability rating scheme to larger forested units of land and reported reasonably good correlations of the whole unit with empirical data of budworm damage.

The somewhat different results in Newfoundland may have been caused by the nature of the outbreak, the characteristics of budworm moth flights, and the characteristics of Newfoundland forests. Blais et al. (1981) reported severe defoliation for several years in large regions of Newfoundland. The extent of damaged forested land (Raske et al. 1982) is evidence of a severe outbreak. Under such severe conditions, weak relations between budworm damage and forest type are likely to be erased.

Budworm moth transport during outbreak years tends to be massive and to occur consistently every year (Greenbank et al. 1980). Newfoundland has received moths by mass transport from the Maritime provinces (Dobesberger et al. 1983) and has likely received several massive moth flights during the last outbreak (Greenbank et al. 1980; Blais et al. 1981). Budworm moths in long-range transport descend to forested land by dawn or early morning. However, the distance between the mainland and Newfoundland is such that normally the moths would barely reach the western part of the island by that time. Nevertheless, all forested land is inundated with moths when a massive moth flight has descended on an area and all forest types are severely damaged. Therefore, where the moths land is almost a random process, which depends on wind direction and possibly, wind speed. Moths cannot be very selective of stands on reaching Newfoundland because they arrive in the morning when they must land.

Newfoundland's forest differs from much of the remainder of the range of budworm in that it has relatively few tree species. Forested land is essentially spruce-fir forests with scattered birch, larch, and a few aspen. Thus, Newfoundland has only a small range of absolute differences in stand composition compared to other regions in eastern North America, and strong relations within this small range may not exist in severe outbreaks.

Our conclusions about vulnerability should not be applied to discussions about susceptibility. Vulnerability is the probability of a stand being damaged in the course of an outbreak; susceptibility is the probability of a stand with sparse populations giving rise to outbreak populations.

Rating vulnerability of Newfoundland's forests by stand types should not be based on the data of the outbreak in the 1970s. Vulnerability not only depends on having acceptable host present but also on how susceptible and vulnerable is the forest upwind of a region.

Literature Cited

Blais, J.R.; Archambault, L. 1982. Rating vulnerability of balsam fir to spruce budworm attack in Quebec. Can., For. Serv., Laurentian For. Res. Centre, Sainte-Foy, Que. Inf. Rep. Lau-X-51. 19 p.

Blais, J.R.; Kettela, E.G.; Moody, B.H. 1981. History of spruce budworm outbreaks in eastern North America with special reference to Newfoundland. Pages 12-17 *in* J. Hudak and A.G. Raske, eds. Review of spruce budworm outbreak in Newfoundland — its control and forest management implications. Can. For. Serv., Newfoundland For. Res. Centre, St. John's, Nfld. Inf. Rep. N-X-205.

Dobesberger, E.J.; Lim, K.P.; Raske, A.G. 1983. Spruce budworm (Lepidoptera: Tortricidae) moth flight from New Brunswick to Newfoundland. Can. Entomol. 115:1641-1645.

Greenbank, D.O.; Schaefer, G.W.; Rainey, R.C. 1980. Spruce budworm moth flight and dispersal: new understanding from canopy observations, radar, and aircraft. Mem. Entomol. Soc. Can. 110. 49 p.

MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56:213-221.

MacLean, D.A. 1982. Vulnerability rating of forests in New Brunswick and Nova Scotia to budworm attack. Can. For. Serv., Maritimes For. Res. Centre, Fredericton, N.B. Inf. Rep. M-X-132. 21 p.

Raske, A.G.; Clarke, L.J.; Sutton, W.J. 1982. The status of the spruce budworm in Newfoundland in 1981. Can. For. Serv., Newfoundland For. Res. Centre, St. John's, Nfld. Inf. Rep. N-X-210. 49 p.

Discussion Group B — Hazard Rating

The Hazard-Rating System for Michigan's Upper Peninsula: A Synopsis of its Development

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Michigan foresters have emphasized silvicultural techniques (Flexner et al. 1983) to minimize impact of spruce budworm (*Choristoneura fumiferana* (Clem.)) on balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moench) Voss). But to set priority for cultural treatment, foresters must be able to identify those stands most likely to incur damage. This was the objective of our hazard-rating system.

We developed Michigan's hazard-rating system empirically because the population dynamics of the budworm and the interactions of the insect, host tree, and site in Michigan were not well understood. A hazard-rating system based on apparent or correlative relations does not necessarily imply cause and effect between the independent and dependent variables. Understanding of the underlying ecological relations, however, may improve the predictive abilities of the model or models developed.

System development was to be relatively simple: collect and analyze data from a series of permanent plots in Michigan's Upper Peninsula; construct empirical, quantitative predictive model or models; collect an independent data set; validate, refine, and implement the predictive model or models in the form of a hazard-rating system (Witter and Mog 1981). The actual development procedure became much more involved. Model validation required numerous returns to the initial development stage, and the procedure evolved into a cyclic pattern of data collection, analysis, validation, and refinement (Figure 1) (Lynch et al. 1984a). Our experiences illustrate the importance of validation in the building of pest management models.

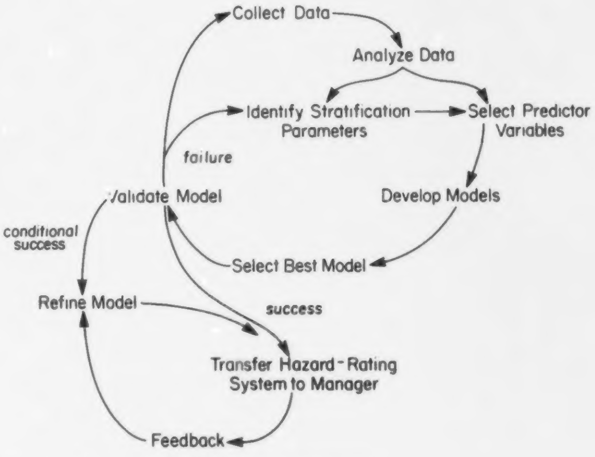

Figure 1. The steps in model development.

One problem encountered in model development and validation was the extreme variability in host distribution, stand character and structure, site conditions, and budworm impact. Balsam fir occurs in extensive areas of spruce-fir forest, as isolated individual stands, and as a component in mixed woods. The proportion of stand basal area represented by balsam fir ranged from 0 to 90 percent in our samples. The age distribution of the host species varied considerably both within and between stands. Stands occurred on a variety of site and soil types — from organic wetlands and poorly drained clay flats to droughty outwash sands. The growing season ranges from 60 to 140 days throughout the peninsula. The interactions of these factors made it extremely difficult to develop models that would accurately predict impact.

Between-stand variability was influenced by the quantity of balsam fir basal area present, stand species composition, and site factors, particularly those indicative of soil moisture availability. Differences in impact between geographic zones appeared to be influenced by differences in topography, climate, forest structure, management intensity, and the duration of the outbreak between regions. The precision and accuracy of the empirical models might be increased if the data were stratified by soil type, by stand species composition, or by the quantity of balsam fir in the stands. Meaningful stratification, however, frequently resulted in too few samples in one or more stratum, too many strata for practical implementation, or a suitable model for one stratum but not another.

Our efforts were also hampered by a lack of historic information on both the stands and on the budworm infestations within each stand. The amount of cumulative defoliation resulting in a specific rate of mortality varies considerably (Blais 1958), but we were unable to determine how many years each stand had been defoliated. Also, we were unable to examine insect-host interactions in Michigan directly because insect population-density estimates were not available.

These limitations notwithstanding, we developed an empirical hazard-rating system for Michigan's Upper Peninsula. Two linear models and two mean values were produced to estimate potential impact in three geographic regions, with one region further stratified by the quantity of balsam fir stocking per stand (Lynch et al. 1984b; Witter and Lynch 1985). Stands can be indexed or ranked according to estimated losses, and priorities established for preventive, presalvage, and salvage harvest operations or for remedial treatments. The system could be easily implemented because the necessary data are readily available from routine compartmental examinations and inventory systems. We believe that the hazard-rating system will be a useful management tool for forest managers.

Literature Cited

Blais, J.R. 1958. The vulnerability of balsam fir to spruce budworm attack in northern Ontario, with special reference to the physiological age of the tree. For. Chron. 34:403-422.

Flexner, J.L.; Bassett, J.R.; Montgomery, B.A.; Simmons, G.A.; Witter, J.A. 1983. Spruce-fir silviculture and the spruce budworm in the Lake States. Mich. Coop. For. Pest Manage. Program Handb. 83-2. 30 p.

Lynch, A.M.; Fowler, G.W.; Witter, J.A. 1984a. Development of empirical models to rate spruce-fir stands in Michigan's Upper Peninsula for hazard from the spruce budworm (Lepidoptera: Tortricidae): a case history. Great Lakes Entomol. 17(3):163-174.

Lynch, A.M.; Witter, J.A.; Fowler, G.W. 1984b. Spruce budworm information leaflets for the Lake States. XI. A hazard-rating system for Michigan. Mich. Coop. For. Pest Manage. Program. Leafl. 84-5.

Witter, J.A.; Lynch, A.M. 1985. Rating spruce-fir stands for spruce budworm damage in Eastern North America. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 636.

Witter, J.A.; Mog, T.P. 1981. An integrated approach for assessing spruce budworm damage and developing a hazard-rating system and stand models for spruce-fir stands in Michigan's Upper Peninsula. Pages 45-52 *in* R.L. Hedden, S.J. Barras, and J.E. Coster, tech. coords. Hazard-rating systems in forest insect pest management: symposium proceedings. U.S. Dep. Agric., For. Serv., Washington, D.C. Gen. Tech. Rep. WO-27.

Discussion Group B —
Hazard Rating

Rating Stand Susceptibility to Western Spruce Budworm

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Attempts have been made in several studies to develop stand hazard-rating schemes for western spruce budworm but the resulting models all have a large amount of unexplained variation and are, at best, only locally applicable. These models lack explicit recognition of certain important habitat attributes and the interaction among independent variables is not represented. The small data sets used in these studies span a limited range of stand conditions and the sampling designs do not account for the temporal and spatial dynamics of infestations. Moreover, host tree defoliation, the most common dependent variable, is difficult to measure consistently and often does not reflect population size and vitality on a unit area basis. Numerous other studies have related certain site, tree, and stand characteristics to budworm survival or host damage. When the significant independent variables from all studies are compared and interpreted in light of the processes that govern budworm survival, a great deal of commonality can be recognized. From this holistic picture of budworm habitat quality and our own field observations, my colleagues and I conceptualized a model that will index stand susceptibility across the full range of forest conditions associated with western spruce budworm.

The susceptibility indexing model reflects the composite interaction of eight stand characteristics in defining budworm habitat quality. These characters, the variables we chose to represent them, and the potential range of index values for each variable are shown in Table 1.

We selected variables that are comparable across all sites and stand conditions and that could easily be derived from widely available forest inventory data. Within these constraints the variables approximate the operational environment of budworm with reference to the effects of climate, predators and food supply. The index values for each variable represent a score for the referenced habitat components. Stand susceptibility increases as: 1) host stocking and climax host stocking increase; 2) total stand density increases; 3) crown class structure becomes more variable; 4) stand vigor decreases; 5) stand age increases; 6) site and regional climate becomes warmer and drier; and 7) the host type in surrounding stands increases.

In the real world habitat components are of varying importance to the success of a population, and provided that certain essential elements are minimally represented, the contribution of any single component to overall habitat quality is highly dependent on the other components. To represent this interaction among habitat components, we decided that the index values for each variable would be multiplied together to yield a composite score for a stand. With all variables set at optimum for budworm, we assigned the maximum index values to reflect our perception of the relative importance of each variable in defining overall habitat quality. While maintaining this weighting, we balanced these maximum values such that their multiplicative total would equal 100. Index values were then scaled across the conceivable range of each variable, reflect-

Table 1
Stand characteristics, variables, and index values for the Stand Susceptibility Model

	Character	*Descriptive Variable*	*Index Value Range*
1.	*Species Composition*	*% host crown cover and* *% climax host crown cover*	*0 – 2.4* *0.6 – 2.4*
2.	*Stand Density*	*total percent crown cover*	*0.8 – 1.6*
3.	*Crown Class Structure*	*coefficient of variation of host tree heights*	*0.9 – 1.7*
4.	*Stand Vigor*	*B.A. stocking/av. max. B.A. and incidence of stress inducing pests*	*0.9 – 1.6*
5.	*Stand Maturity*	*B.A. weighted mean host tree age*	*0.3 – 1.3*
6.	*Site Climate*	*habitat type group*	*0 – 1.5*
7.	*Regional Climate*	*geographic location*	*0 – 1.2*
8.	*Surrounding Hosts Type Continuity*	*% host type in surrounding 1000 acres and adjacent to the stand*	*0.6 – 1.7*

ing the reduced contribution or detraction from optimal habitat as the habitat components referenced by each variable become limiting to budworm survival.

Thus the stand susceptibility model is a conceptual representation of budworm habitat quality which scores a stand on a relative scale of 0-100. We used both inductive and deductive reasoning in constructing this model; resolving the apparent disparities among correlation evidence by comparison to the life processes known to influence budworm survival on one hand, and then by defining a function role for budworm infestations that is consistent with the principles of ecosystem succession and rejuvenation. Documentation of this rationale can be found in a forthcoming CANUSA-West publication entitled *Western Spruce Budworm*.

From a research standpoint the model serves as a working hypothesis which should receive rigorous validation. From an operational standpoint the model performs reasonably well in distinguishing relative stand susceptibility while pointing out those stand variables which are amenable to silvicultural manipulation.

Discussion Group B —
Hazard Rating

Why Risk Rate Sites and Stands Using Multivariate Regression Models?

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Multivariate regression models that predict pest hazards from descriptive characteristics of sites and stands are considered useful for: 1) conceptualizing the environment of pest-outbreak prone site-stand configurations; 2) designing silvicultural measures to reduce pest hazards; and 3) risk-rating existing stands in terms of current or future pest hazards.

We have discussed the applicability of multivariate hazard models for (1) and (2) elsewhere in the symposium. In this paper we address the potential usefulness of empirically derived models for hazard-rating purposes. The case examples are models portraying the relationships of western spruce budworm defoliation levels to forest site-stand attributes in Idaho.[1]

Model formulations from the Clearwater National Forest study area (Table 1) show that the environmental setting of studied site-stand characteristics bears decisively on model formulation. Pest hazard models developed in one ecological setting (vegetation series) are not applicable for hazard-rating purposes in a different setting.

This lack of transferability is further underscored by the model developed in another study area on the Salmon National Forest. The Salmon model (Table 2) differs from the Clearwater models not only in coefficient estimates but also in functional relationships between the dependent variable and the independent, risk-predictive variables.

Why do these differences in model formulation exist? The reasons are likely manifold: differences in geology, soils and corresponding differences in the developmental dynamics of the forest; differences in management and forest use history; and differences in genetic make-up of host trees and budworm populations. Considering the chemical and behavioral nature of plant-herbivore interactions, it seems presumptuous to expect that prediction models valid for assessing budworm risk throughout the insect's range could be developed through correlation of budworm population indices with descriptive characteristics of sites and stands.

Why then spend considerable effort on development of such models? The justification lies foremost in model usefulness for conceptualization purposes. Model development is a logical and practical "first step" toward understanding the operational environment of habitats favoring budworm population increases. The applicability of the quantitative models as tools to rank site-stand configurations in terms of current and future hazard potential is limited to the range of conditions from which they were derived. However, when used in connection with the derived conceptual insights, the

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[1] Stoszek, K.J. and P.G. Mika. 1983. The relationships of western spruce budworm outbreaks to site/stand attributes; development and management history: Model completion and comparison. CANUSA-West final report. CANUSA Spruce Budworm Program-West, Portland, OR. 70 p.

Table 1
Multiple regression model for budworm defoliation within the western hemlock (WH) and subalpine fir (SAF) vegetation series on the Clearwater National Forest of central Idaho

	Coefficient		*Variable*
	WH	*SAF*	
Percent defoliation/host =	*23.4386*	*121.3052*	*Intercept*
	0.0122	*−0.0144*	*Elevation*
	−24.9818	*28.9354*	*Small fuel load*
	−0.0195	*0.0679*	*Crown competition factor*
	−5.7295		*Ln (standard deviation of tree age)*
	−0.1132		*Average tree age*

$R^2 = 0.7181$ $MSE = 72.3149$ $F = 14.43$ $P > F = 0.0001$

Table 2
Multiple regression model for budworm defoliation on the Salmon National Forest of central Idaho

Percent defoliation/host = -331.8777

$+ 0.1226 \times \text{elevation}$

$- 0.1029 \times 10^{-4} \times \text{elevation}^2$

$+ 6.5873 \times \text{host BAI}$

$R^2 = 0.5111$ $MSF = 70.8238$ $F = 15.68$ $P > F = 0.0001$

models may be useful in developing systems to index budworm hazard site-stands in other, ecologically similar areas.

The following conclusion may help in such a process. The models we developed from ground surveys and similar models developed through aerial photo interpretation by others[2] suggest that budworm population levels in a given geographic and environmental setting are associated with both certain sites and certain states of the forest. This indicates that conditions conducive to budworm population increases are functionally related to certain states of the dynamically changing forest and host-tree system (predisposition state), and that these predisposition states occur with higher probability on certain (risk-prone) sites.

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[2] Heller, R.C., J.J. Ulliman, and H.N. Anderson. 1981. Use of photo interpretation and remote sensing techniques to establish hazard rating criteria for spruce budworm susceptible stands. CANUSA-West final report, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow. 48 p.

Ulliman, J.J. and B.L. Kessler. 1983. Validation of a spruce budworm aerial photo/risk model. CANUSA-West final report. CANUSA Spruce Budworm Program-West, Portland, OR. 87 p.

Discussion Group B — Hazard Rating

Summary

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Hazard rating may be an ill-defined term because the concept is closely linked to both susceptibility and vulnerability, the subject of the previous workshop, and to silvicultural strategies which are discussed in the next workshop this afternoon. However, hazard rating may be defined as a ranking of stands according to their susceptibility to the budworm in order to set priorities for silvicultural treatments. This ranking should integrate site and stand conditions known to influence the budworm and should be usable throughout a forest type or series.

In this workshop, we have reviewed some hazard-rating systems used in Newfoundland, Michigan, and in the northern Rocky Mountains.

Newfoundland Forests Vulnerable to Spruce Budworm

The character of Newfoundland's forests differs from much of the remainder of the range of the budworm in that Newfoundland's forests have relatively few tree species; forested land is essentially spruce-fir forests with scattered birch, larch, and a few aspen. Thus, there is only a small range of absolute differences in stand composition compared to other regions in eastern North America.

There are at least three reasons for the somewhat different aspects of hazard rating in Newfoundland. The characteristics of the forests is one element and the nature of the outbreak is another. The most important, however, is the characteristics of budworm moth flights.

During outbreak years, moth transport tends to be massive and to occur consistently every year. Budworm moths are transported long range at night and descend on forested stands upwind of their origin by dawn or early morning. These moths arrive in Newfoundland from the Maritime provinces on the mainland and the deposition of moths is not a selective but rather a random process, depending upon wind direction and possibly wind speed.

Therefore, strong hazard-rating and vulnerability relationships do not exist in severe outbreaks because all forested lands are inundated with moths when massive moth flights descend on an area and severely damage all forest types and mask stand vulnerability. On the other hand, when flights do not occur, or when flights do not settle on any given area, stand vulnerability relationships do hold up.

Hazard-Rating for Michigan's Upper Peninsula

The objective of the hazard-rating system in Michigan was to provide forest managers with a decision-making tool. Investigators consider hazard-rating as a process to identify those stands most likely to incur damage. They developed Michigan's system empirically because the population dynamics of the budworm and the interactions of the insect, host tree, and site were not well understood. Two linear models and two mean values were produced to estimate potential impact in three geographic regions.

The greatest difficulties encountered in the development of the system were: 1) variability in the distribution of host species; 2) the character, structure, and conditions of the site and stand; 3) the impact of the budworm, especially differences between the geographic zones; 4) the lack of historic information on stands and on the infestations within each stand; and 5) the range of growing season throughout the peninsula.

Michigan investigators believe that their hazard-rating system will be a useful tool for managers and have validated the models in their system. Stands can be indexed or ranked according to estimated losses and subsequently be prioritized for preventative, presalvage or salvage harvest operations.

Hazard-Rating Systems for the Northern Rocky Mountains

Three hazard-rating systems have been developed for the northern Rockies — a ground survey system, an indexing system, and an aerial photography system. Only the first two have been discussed and compared in this workshop. Since the aerial photography system uses the ground estimates of defoliation from the ground survey, the two systems become similar.

The ground survey system (model) is based on regression analyses from site, stand, and defoliation data collected in the field. Only trees ≥ 3.0 inches dbh were used in calculating the statistics and no stands younger than 40 years of age were included in the sample base.

The interpretation of results leading to recommendations for silvicultural systems are hypotheses at this time. These hypotheses are based on the regression analyses and knowledge of the forest ecosystem.

It is very important to recognize that these ground survey models are for specific circumstances or infested forests within outbreak areas and the models are only applicable to the forests where the data were collected and are not transferable to other ecological regions.

The indexing system model was conceptualized by western investigators — using all of the insect-host relationships known, existing forest inventory data, the available literature and their field experience and observations — to index stand susceptibility across the range of the western budworm in the northern Rockies. The model was intuitively derived and as such serves as a working hypothesis that seems to give reliable, albeit imprecise, indications.

The stand susceptibility model (indexing model) gives a relative index of western budworm habitat quality and references directly or indirectly the quantity and quality of available food, the action of budworm predators, and the effects of climate.

There are some areas of disagreement over the interpretation of results between the two hazard-rating systems — the ground system and the indexing system — but their theories are in some areas mutually inclusive. Since both rating systems are based on the best information available at this time — and the interpretation of that information — refinements, further developments, and closer agreement of these concepts should be expected in the future.

Discussion Group C — Silvicultural Strategies to Reduce Susceptibility/ Vulnerability

Considerations for Design of Silviculture Measures to Reduce Western Spruce Budworm Hazard

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Two information items are important for design of silvicultural regimes that aim at modification of budworm hazard-prone conditions. One involves identification of site-stand configurations with high budworm risk. The other pertains to possible causes of outbreak-prone forest conditions. This knowledge can be expediently gained through development and interpretation of budworm-hazard models. The budworm defoliation hazard models developed in Idaho indicate that host trees sustain heavier defoliation in stands on land with certain features and under certain structural and developmental configurations.[1] Model formulations differ with environmental conditions as portrayed by vegetation series. In stands on cool, high-elevation, subalpine fir series, defoliation decreased with elevation and increased with stand density and amount of woody residue on the ground. The opposite occurred on warm, moist, western hemlock series located in low to mid-elevations. In both series, defoliation was inversely related to average stand age and tree age deviation from the average. In Douglas-fir series of south-central Idaho, host stands with high budworm risk were of low density, with no duff on the ground, and with host trees exhibiting good but declining growth rates. Highest defoliations occurred at elevations of about 6,000 feet (1800 m).

The high-risk, site-stand configurations are perceived as conducive to budworm population increase. Deductive interpretations of possible ecophysiological conditions of outbreak-prone habitats led to the concept that budworm outbreaks are symptoms of a forest system in which the nutrient cycle is temporarily (through climatic stress) or permanently discoupled (*sensu* Ulrich 1982). The ensuing nutrient stress in host trees results in changes in foliage quality favoring budworm population release.

Silvicultural Risk-Reducing Considerations

Decisions on silvicultural systems and practices best suited to reduce budworm hazard should consider the expected budworm outbreak frequency for a given area (Kemp 1983), the predicted severity of defoliation, and the possible causes of host predisposition to herbivory in a given high-risk setting. On the premise that nutrient stress is a key factor in budworm population increases, silvicultural treatments should focus on increasing the rate of decomposition of organic matter, and increasing the organic matter content and amount of available water and mineral nutrients in the soil.

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[1] Stoszek, K.J.; Mika, P.G. 1983. The relationships of western spruce budworm outbreaks to site-stand attributes, development and management history: model completion and comparison. Coll. For., Wildl. and Range Manage., Univ. Idaho, Moscow. CANUSA-West Budworm Program, Final Rep. 70 p.

Selection silvicultural systems appear best suited to reduce budworm hazard by improving soil organic matter content, cation exchange capacity, and availability of moisture and nutrient. Converting stands to a regulated, uneven-aged structure should be considered as a potential budworm hazard remedy on cool, low-productivity sites and on warm, dry sites, but only in areas with low to moderate outbreak frequency (more than 11 years without outbreaks) to permit seed production and regeneration development.

In host-dominated stands in the cool, subalpine fir series, the goal is a target structure characterized by about 1.6 q-factor and a basal area per acre of about 100 square feet. This structure would keep the amount of biomass sufficiently low to prevent excessive tie-up of nutrients and permit vigorous growth of the younger components in the stand. The temperature and moisture regime of such stands should facilitate decomposition of organic matter and increase available nutrients in the soil. The ecophysiological environment of stands under selection management is apt to resemble that of stands in the aggradation phase of the subclimax stage of succession to which subalpine fir is best adapted. In addition, the structure of the uneven-aged forest is known to provide prime habitat conditions to budworm predators.

On the warm, dry Douglas-fir series, a target structure characterized by a 1.2 to 1.5 q-factor and 50 to 80 square feet basal area/acre appears appropriate to generate conditions less conducive to increases in budworm population.

A conversion strategy in which selection for vigor is more important than fast attainment of the specified target structure appears advisable in both situations, as long as the goal of improved nutrient availability is not jeopardized.

Stand conversion to a selection structure is impractical in areas with high frequency of outbreaks because of severe impacts of budworm on reproduction. Here, in accordance with Schmidt et al. (1983), consideration must be given to the biological and economic feasibility of applying even-aged harvest-regeneration methods to transform a budworm host-dominated stand structure to one dominated by nonhost trees. On warm, moist and cool, productive sites, even-aged systems favoring mixed-species stands composed of shade-intolerant species adapted to seral conditions of the given site appear appropriate for reducing budworm hazard. Harvest-regeneration practices must be executed with care so that site productivity is maintained. Stand conversion to nonhost species should be considered on high-risk sites in areas with high outbreak frequency.

Literature Cited

Kemp, W.P. 1983. The influence of climate, phenology, and soils on western spruce budworm defoliation. Ph.D. dissertation. University of Idaho, Moscow, ID. 143 p.

Schmidt, W.C.; Fellin, D.G.; Carlson, C.E. 1983. Alternatives to chemical insecticides in budworm susceptible forests. Western Wildlands, University of Montana, Missoula, MT. 9(1):13-19.

Ulrich, B. 1982. A concept of forest ecosystem stability and acid deposition as a driving force of destabilization. Pages 1-29 *in* Ulrich and Pankrath, eds. Effects of accumulation of air pollutants in forest ecosystems. D. Reidel Publ. Co., Boston. 389 p.

Discussion Group C —
Silvicultural Strategies to
Reduce Susceptibility/
Vulnerability

Building New Spruce-Fir Stands — A Long-Term Localized Strategy for Reducing Spruce Budworm Impact

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A comprehensive silvicultural strategy aimed at minimizing future spruce budworm damage must be started well in advance of a serious budworm problem. Silvicultural treatments designed to maximize the proportion of less vulnerable spruce and to increase growth and vigor, create stand conditions that allow for several action options should budworm attack occur. If treatments are delayed until an outbreak strikes, actions are limited to presalvage and salvage operations, usually with major losses in yield.

Research in Maine suggests that mature spruce-fir stands with as little as 11 percent spruce growing stock can be naturally regenerated by the shelterwood method (Table 1). These stands can then be cultured into new stands containing a higher percentage of the more desirable spruce than was originally present (Frank 1977, 1983). The regeneration phase may require 10 years or less in previously managed stands to as long as 20 years in unmanaged stands (Figure 1). An initial thinning should be made 5 to 10 years after establishment, when the new crop averages about 2 m (6.5 ft) to 3 m (10.0 ft) in height. Potential crop trees of desirable species, vigor, and form should be selected and adequate growing space provided by removing unwanted and competing trees. The resulting residual stand, newly reconstructed and better able to resist budworm attack, should now contain from 40 to 75 percent or more spruce.

Table 1
Shelterwood strategies and spruce responses during the regeneration phase for four shelterwood trials being conducted on the Penobscot Experimental Forest near Bangor, Maine

	Shelterwood strategy			
	2-stage, no TSI		*3-stage, with TSI*	
Item	*Stand 21*	*Stand 30*	*Stand 23*	*Stand 29*
Strategy — Growing stock basal area and percent removed (m^2/ha)[1]				
At first harvest	*28.6-42% (1957)*	*31.0-43% (1957)*	*25.0-31% (1955)*	*30.2-34% (1957)*
At second harvest	*Not applicable*	*Not applicable*	*24.0-74% (1966)*	*26.5-62% (1968)*
At final harvest	*22.0-84% (1967)*	*22.8-92% (1967)*	*9.3-100% (1972)*	*12.0-100% (1974)*
Spruce responses — Spruce as a percentage of total growing stock basal area				
At first harvest	*15% (1957)*	*17% (1957)*	*11% (1955)*	*25% (1957)*
In regeneration phase	*23% (1963)*	*28% (1963)*	*42% (1967)*	*64% (1968)*
At final harvest	*24% (1967)*	*28% (1967)*	*41% (1972)*	*55% (1974)*
Spruce responses — Percent milacre stocking of spruce seedlings between 30 cm in height and 1.27 cm in diameter at breast height[2]				
In regeneration phase	*7% (1965)*	*3% (1964)*	*2% (1965)*	*2% (1954)*
At final harvest	*Not available*	*Not available*	*24% (1972)*	*35% (1974)*
After final harvest	*13% (1970)*	*20% (1970)*	*24% (1972)*	*22% (1975)*
After final harvest	*70% (1982)*	*72% (1981)*	*60% (1980)*	*82% (1982)*
After spacing[3]	*Not spaced*	*Not spaced*	*40% (1981)*	*75% (1983)*

[1] One square metre per hectare equals 4.356 square feet per acre.
[2] One centimetre equals 0.393701 inch.
[3] Including seedlings larger than 1.27 cm dbh.

Young stands containing rapidly growing spruce and fir trees should develop into healthy, merchantable stands in half the time required for unmanaged stands. Treated stands with short rotations, with the best spruce trees reserved to the end of the rotation, should reduce the area occupied by overmature and dense balsam fir — conditions often cited as being difficult to manage during a spruce budworm outbreak. Less vulnerable stands may create a less susceptible forest.

Cultured stands, managed throughout a rotation, should provide the forest manager with a less complex management situation. Protection against the budworm is simplified, and the lead time for decision making and action programs designed to lessen damage impact are lengthened. The net result is more wood in the local woodpile and less wood lost to the budworm.

Literature Cited

Frank, R.M. 1977. Indications of silvicultural potential from long-term experiments in spruce-fir types. Pages 159-177 *in* Proc. of the symposium on intensive culture of northern forest types, Orono, ME., 20-22 July 1976.

Frank, R.M. 1983. A focus on natural regeneration methods for developing a spruce-fir forest less vulnerable to spruce budworm. Abstract *in* Proc. of the 1983 Eastern Spruce Budworm Research Work Conference, Orono, ME., 10-11 Jan. 1983.

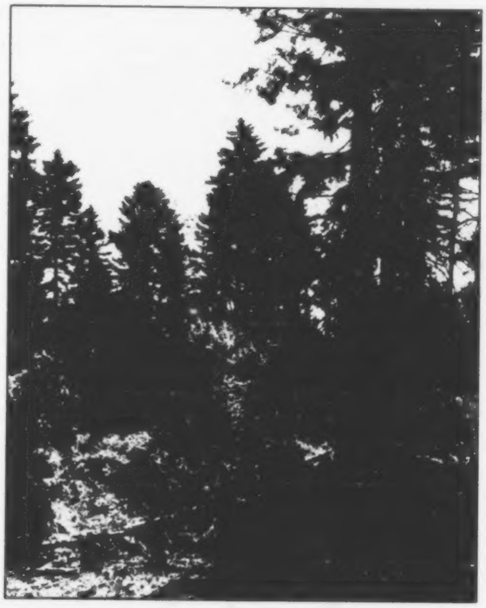

Figure 1. Three-stage shelterwood two growing seasons after the second harvest, which removed 74 percent of the growing stock. Note residual red spruce seed trees. Penobscot Experimental Forest, Maine.

Discussion Group C —
Silvicultural Strategies to
Reduce Susceptibility/
Vulnerability

Silviculture — Solution to Budworm Problems in the Inland Mountain West

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The long-term solution to any problem lies in reaching a better understanding of all factors surrounding that problem. The western spruce budworm problem has plagued forest managers in the inland Mountain West since the middle of this century and is no exception to that rule. Attempts at short-term solutions to budworm problems have been less than successful because ecological relations of budworm and the host forests have been poorly understood (Fellin et al. 1983). Much is still unknown, but enough information is accumulating to allow more rational management decisions in dealing with the budworm.

Without altering the character of the forest — which provides all the substrate needed by the budworm — logically only short-term relief can ever be expected from direct control efforts (Fellin 1983). Everything the budworm needs is still there.

Silvicultural methods can be used to alter the character of the host forests and, as a result, provide long-term relief. Two straightforward principles are involved: the silvicultural methods must create conditions more favorable for forest vigor and development and less favorable for budworm survival (Carlson et al. 1983). Creating favorable conditions for forest growth and development is routinely done in properly prescribed silvicultural practices. Making conditions less favorable to budworm has had inadequate consideration, in part because of reliance on insecticides, and also because the relations between silvicultural practices and budworm were not fully recognized.

Silvicultural practices can be used to affect nearly all phases of the budworm life cycle. For example, practices that discriminate against the shade-tolerant species, favorite hosts of the budworm, reduce the food supply, egg-laying sites, and favorable landing sites for dispersing larvae. Practices that alter the vertical and lateral structure of residual stands can increase larvae mortality during dispersal.

Even-aged management practices best meet the silvical requirements of most commercial forests of the inland Mountain West. In addition, they also create conditions least favorable to the western spruce budworm because they favor seral species, which are primarily nonhosts, and discriminate against the climax species that are primary hosts of budworm (Schmidt et al. 1983). Even-aged management also largely eliminates the continuous layering of host species so favorable for budworm survival during dispersal.

A half century of effective fire control and economic selection cuttings over vast areas of the West accelerated succession toward climax forests composed primarily of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), the spruces (*Picea* spp.), and the true firs (*Abies* spp.) — all primary hosts of the budworm. The real challenge now lies in implementing silvicultural practices throughout budworm host forests that will reverse the trends set in motion earlier for much of this century. Fortunately, practices that best meet the silvical requirements of most of our most important conifers are those that also result in forests least desirable for the budworm.

Literature Cited

Carlson, C.E.; Fellin, D.G.; Schmidt, W.C. 1983. The western spruce budworm in northern Rocky Mountain forests: a review of ecology, insecticidal treatments and silvicultural practices. Pages 76-103 *in* J. O'Loughlin and R.D. Pfister, eds. Management of second-growth forests: the state of knowledge and research needs. Proc. Symp., Montana Forestry and Conservation Experiment Station, University of Montana, Missoula, MT.

Fellin, D.G. 1983. Chemical insecticides vs. the western spruce budworm: after three decades, what's the score? Western Wildlands, University of Montana, Missoula, MT. 9(1):8-12.

Fellin, D.G.; Shearer, R.C.; Carlson, C.E. 1983. Western spruce budworm in the northern Rocky Mountains: biology, ecology, and impacts. Western Wildlands, University of Montana, Missoula, MT. 9(1):2-7.

Schmidt, W.C.; Fellin, D.G.; Carlson, C.E. 1983. Alternatives to chemical insecticides in budworm-susceptible forests. Western Wildlands, University of Montana, Missoula, MT. 9(1):13-19.

Discussion Group C —
Silvicultural Strategies to
Reduce Susceptibility/
Vulnerability

Summary

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Silviculture can be loosely defined as the "art and science of manipulating the development of forest vegetation toward attainment of realistic management goals." In this context, silviculture is thought to have the potential to render budworm-susceptible and vulnerable stands "budworm proof." Is this expectation realistic? According to contributors to this workshop, it is at least an objective worth trying to attain. Robert Frank and Marcia McKeague[1] outlined strategies against the spruce budworm (*Choristoneura fumiferana* (Clem.)) in the East. They emphasized reduction of budworm effects on stands with high risk and high value through timely harvest or thinnings in favor of spruce. Even-age harvest-regeneration methods and practices designed to regenerate spruce-dominated stands are recommended. Short rotations and intensive culture of spruce are expected to increase resistance and reduce vulnerability of future stands to the budworm. The speakers also believe that higher intensity of management associated with higher diversity in age-class distribution may increase budworm dispersal losses and consequently reduce the severity of outbreaks.

The silvicultural strategies against the western spruce budworm (*C. occidentalis* Freeman) presented by Wyman Schmidt and myself aim at modifying stand conditions that seem to favor increases in budworm population into less favorable configurations. We agree on silvicultural remedies for the budworm on the productive sites used to produce commercial timber; here, even-age silvicultural systems that establish and maintain vigorous cultures of seral tree species should produce relatively budworm-proof stands. We disagree on the reasons for stand susceptibility to the western spruce budworm, however. Schmidt and his coworkers (See Carlson et al., these proceedings), think that moisture stress and the stand composition and structure of successionally advanced stands that have resulted from fire exclusion and selective logging are at the base of increased host susceptibility to the budworm. These views are reflected in their recommendations.

Based on results of our budworm hazard-rating work (Stoszek and Mika, this workshop), I believe that nutritional stress — of specific but as yet unidentified nature — in host trees is the cause of susceptibility to the budworm. As a consequence, I emphasize treatments that can improve rates of nutrient cycling, availability of moisture and nutrients, and host-tree nutrition. Thus, I recommend selection silviculture systems in zones with low to moderate outbreak frequency, especially on low productivity sites with cool or warm, dry climates. I have no good answer to budworm problems on similar sites with high outbreak frequency.

A productive discussion from the floor followed the presentation of these diverse opinions. The consensus was that much more information is needed on host resistance and susceptibility to budworm, and that experimentally substantiated information on soil/host/budworm interactions is needed to design silvicultural strategies for reducing the budworm problem. Without this information, budworm-preventive silviculture is apt to remain in the realm of art — or chance.

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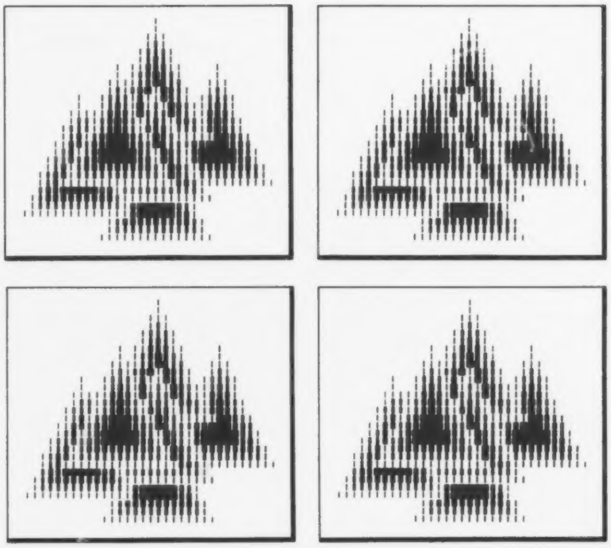
[1] Silviculturist for International Paper Company; oral presentation given on short notice.

Workshop IV — Techniques of Foliage Protection and Population Manipulation

What new or modified techniques are currently available, how effective are they and what developments are in the offing?



Workshop IV — Techniques of Foliage Protection and Population Manipulation

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The session is a review of the tactics now available to forest manager or under research and development, and of the protection strategies integrating those tactics. A strategy is the assembly of tactics used over a period of time — usually several years — to cope with a pest and its effect on wood supply. Budworm outbreaks are so extensive and so ravaging of stand growth and survival, that changes in age-class distribution and in yield curve behavior alter the wood supply expectation for several decades. The goal of a protection strategy is therefore to manipulate budworm distribution and density throughout the outbreak period so that a management unit may continue to sustain the growth rates and inventory needed and planned for industry.

A protection strategy depends upon the reliability of tactics and the vigor with which they are applied. Tactics are the annual or periodic treatments used in designated stands. The ideal tactic is a classical biological control organism which would be self-replicating, self-dispersing, density-dependent and numerically-responsive, and integrated permanently with the ecosystem; no such solution is in current prospect for spruce budworm outbreaks. The available tactics are in two broad classes: chemical control and biorational treatments. The biocidal mechanisms and environmental implications of these two classes differ sharply, but they share the same application technology and the same objective — to reduce budworm density in a target area. Within each class, some tactics are aimed at an immediate reduction in current damage; others aim at a delayed population suppression by reducing survival or reproduction at vulnerable stages.

CANUSA planners recognized from the beginning the need for intensified development of treatment tactics, and formulated targets for the development and evaluation of chemical and microbial insecticides, and for application technology (Target 4, CANUSA Plan). Thus the CANUSA Symposium incorporates two broad state-of-the-art reviews: chemical insecticide tactics and strategies by J.A. Armstrong, and the status of biorationals, by J.C. Cunningham, both of the Canadian Forestry Service. Both papers incorporate historical reviews, an assessment of the CANUSA contribution, and an evaluation of current technical capability.

Those reviews are expanded by discussion papers focusing on the state of research and development in specific areas. The group coordinated by J. Robertson (USDA Forest Service) discussed the development and

La séance porte sur les tactiques auxquelles peuvent maintenant recourir les aménagistes ou qui font l'objet de travaux de recherche-développement et sur les stratégies de protection qui englobent ces tactiques. Une stratégie est un ensemble de tactiques qui, habituellement pendant plusieurs années, servent à juguler un ravageur et les dégâts qu'il cause aux réserves de bois. Les infestations de la tordeuse couvrent un territoire si étendu et elles sont si néfastes à la croissance et à la survie des peuplements que les changements de la répartition des classes d'âge et de l'allure de la courbe de production modifient l'approvisionnement prévu en bois pour plusieurs décennies. Le but d'une stratégie de protection est donc de modifier la répartition et la densité des effectifs de la tordeuse durant la période d'infestation de sorte qu'une unité d'aménagement pourra continuer à maintenir le rythme de croissance et le volume des stocks nécessaires et prévus pour l'industrie.

La stratégie de protection dépend de la fiabilité des tactiques et de la vigueur de leur exécution. Les tactiques sont les traitements annuels ou périodiques appliqués à des peuplements désignés. Idéalement, elles consistent en la lutte biologique classique au moyen d'organismes capables de se reproduire et de se disperser, dont l'action est réglée sur la densité et les effectifs des populations à juguler et qui, en plus, sont intégrés de façon permanente à l'écosystème; contre la tordeuse, aucune solution du genre n'est actuellement anticipée. Les tactiques actuelles se répartissent en deux grandes catégories: la lutte chimique et la lutte biologique. Les mécanismes biocides et les conséquences écologiques de ces deux catégories diffèrent énormément, mais celles-ci ont en commun les mêmes techniques de traitement et le même objectif: réduire la densité des effectifs de la tordeuse dans une région donnée. Dans chaque catégorie, certaines tactiques visent à réduire immédiatement les dommages actuels; les autres, à réprimer à long terme les effectifs en réduisant la survie ou la reproduction des insectes lorsque ceux-ci sont à un stade vulnérable.

Dès le début, les planificateurs du programme CANUSA ont reconnu le besoin d'intensifier l'élaboration des tactiques de traitement et ils ont fixé des objectifs pour la mise au point et l'évaluation d'insecticides chimiques et microbiens et l'application des techniques de traitement (cible 4 du plan CANUSA). Ainsi, le colloque sur le programme CANUSA fait doublement le point de nos connaissances:

evaluation of chemical insecticides and their formulation. J.B. Dimond (University of Maine) headed the group discussing *Bacillus thuringiensis* (B.t.) parasitoids, pathogenic agents, and pheromones: C. Wiesner (New Brunswick Research and Productivity Council) and colleagues discussed the many faces of application technology: spray transport and deposit, atomization, formulation, navigation, timing and the biological interface. Finally, P. Kingsbury (Canadian Forestry Service) discussed the environmental impact of pest control products and their chemical accountability; this paper was not formally presented at the Symposium itself.

It is evident that all phases of research and development were vigorously pursued during the CANUSA period beginning in 1977. The information available to protection managers has become much stronger and more reliable. But we have by no means arrived at a comfortable research plateau where technology transfer alone would suffice to implement powerful protection strategies, or to offer unambiguous choices of tactical options on the basis of efficacy, safety, and cost. Research needs are still urgent. Forest managers still face uncertainty in adopting rational strategies that integrate forest policy, wood supply imperatives, fiscal restraints, and public support.

par l'aperçu des tactiques et des stratégies utilisant les insecticides chimiques, de J.A. Armstrong, et le point sur la lutte biologique, de J.C. Cunningham, tous deux du Service canadien des forêts (SCF). Leurs communications comprennent un historique et une évaluation de l'apport du programme CANUSA et des possibilités techniques actuelles.

Des documents de travail portant sur l'état de la recherche-développement dans des secteurs précis élargissent la portée de ces communications. Le groupe dont J. Robertson (USDA Forest Service) est le coordonnateur a traité de la mise au point et de l'évaluation des insecticides chimiques ainsi que de leur préparation. J.B. Dimond (Université du Maine) a dirigé le groupe qui a discuté de *Bacillus thuringiensis* (B.t.), des parasitoïdes, des agents pathogènes et des phéromones. C. Wiesner (New Brunswick Research and Productivity Council) et ses collègues ont traité des nombreuses facettes des techniques de traitement: transport et dépôt du nuage pulvérisé, atomisation, préparation, navigation aérienne, choix du moment et du stade de développement des peuplements et de leurs parasites. Enfin, P. Kingsbury (SCF) a traité des répercussions environnementales des antiparasitaires et du bilan de leurs résidus et métabolites; cette communication n'a pas été officiellement présentée durant le colloque.

Il est évident que toutes les étapes de la recherche-développement ont été abordées de façon diligente depuis le déclenchement du programme CANUSA, au début de 1977. Les renseignements dont peuvent disposer les aménagistes chargés de la protection des forêts sont maintenant plus étoffés et plus fiables, mais la recherche n'a pas encore atteint ce plateau où la diffusion de connaissances techniques peut à elle seule suffire à donner lieu à des stratégies efficaces de protection ou à offrir des choix clairs de tactiques qui répondent aux critères d'efficacité, de sécurité et d'économie. Les besoins de la recherche sont encore criants. Les aménagistes sont encore aux prises avec l'incertitude lorsqu'il s'agit d'adopter une stratégie rationnelle qui intègre les données de la politique forestière, les impératifs de l'approvisionnement en bois, les contraintes fiscales et l'appui du public.

Discussion Group A — Chemicals

Early Laboratory Bioassays in Canada

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Efforts to replace DDT began during the mid 1950s because the chemical was toxic to fish. By the early 1960s, phosphamidon was used around watershed areas because it was relatively less toxic to fish. When the use of phosphamidon increased adverse effects on birds were observed.

During the mid-1960s, efforts to replace DDT and phosphamidon with safer materials were intensified. A number of organophosphorous and carbamate compounds were screened in the laboratory; approximately 10-15 compounds were promoted for field testing during this period.

By the end of the 1960s, stabilized natural pyrethrins and pyrethroids were tested in the laboratory and were subjected to field evaluations by the mid-1970s. In the early 1980s aminodihydrazone compounds were introduced and are now being tested in the laboratory. Blair Helson will discuss progress with these chemicals. The organophosphates, fenitrothion, malathion, dimethoate, and the carbamate, mexacarbate, were registered by the late 1960s. Aminocarb, acephate, trichlorfon, and carbaryl were registered during the period from the mid- to late-1970s.

In Canada from the mid-1970s onward, importance was placed on testing different formulations of registered materials because of fear of side effects and health hazards of primary and carrier solvents and emulsifiers. This development also coincided with the reduction of industry's interest in developing new compounds for forestry use. This reduced interest was probably due to environmental problems and escalating cost of developing materials.

During the laboratory screening process, the following factors were considered before promoting materials for field evaluation:

1. High contact toxicity to spruce budworm larvae (LC_{50}, 0.5 or less $\mu g/cm^2$).
2. LT_{50} toxicity of at least 3-4 days, under natural weathering conditions, to 5th instars.
3. Fish toxicity less than that of DDT.
4. Bird toxicity less than that of phosphamidon.
5. Mammalian toxicity more than 50 mg/kg.
6. Cost of the chemical, its availability in large quantities, and its use pattern in agriculture.

Those materials that had very high contact toxicity but poor residual toxicity due to vaporization, hydrolysis and photolysis were not successful in the field trials (e.g., dibrom, methomyl, natural pyrethrins, and early pyrethroids).

Discussion Group A — Chemicals

Estimation of Field Application Rates on the Basis of Laboratory Data

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Because laboratory experiments are relatively inexpensive compared to field trials, many attempts have been made to use data from laboratory bioassays to estimate the application rate necessary to obtain a desired level of mortality of budworm population in the field. Two years ago, we developed a reliable method for using laboratory bioassay data to estimate field application rates. This method culminated almost 20 years of laboratory work.

Early laboratory studies emphasized screening of chemicals by topical application. By comparing the relative contact toxicities of new chemicals to the toxicities of those already field tested, crude extrapolations were made to suggest field application rates for each chemical. This procedure was inherently inaccurate because the measurement units in topical application bear little relationship to the amount actually reaching the insects in the trees.

Laboratory spray chambers were also used to determine contact toxicity. Even though application rates of these sprays were calculated in units equivalent to those applied in the field, the accuracy of extrapolations did not improve because the sprays in these chambers were usually applied to fully-exposed insects. Field application rates were consistently underestimated because factors such as evaporation and shielding of the insects by foliage were not taken into account. In an attempt to compensate for underestimation of the dose actually reaching the insect in the field, a laboratory-based spray dose estimate was multiplied by an arbitrarily chosen factor of 3 to obtain a field application rate (Williams 1973).

Besides contact effectiveness, toxicity by ingestion was also recognized as an important component of overall efficacy. Bioassays were developed to test toxicity by feeding (e.g., Granett and Retnakaran 1977; Gillette et al. 1978), but these data were useful only for determination of relative toxicities and were subject to the same limitations as topical and spray application data.

The first deliberate attempt to integrate data on contact and feeding to predict field effectiveness was a series of bioassays and ranking criteria developed by Robertson and Haverty (1981). Although an improvement over previous attempts such as those of Robertson and Boelter (1979a, b), this method still provided no satisfactory means to estimate field application rates.

Subsequently, multiplication factors for suggesting field application rates for western spruce budworm were derived (Haverty and Robertson 1982). The seven chemicals — acephate, carbaryl, fenitrothion, methomyl, permethrin, sulprofos, and thiodicarb — on which these factors were based had been field tested previously so that a minimum effective dose to cause 90 percent mortality of western spruce budworm in the field was available for each chemical. The bioassay was done by applying sprays to larvae on foliage. The rainfastness of each chemical applied at the ED_{90} was determined to assess the degree to which rainfall affects efficacy. The ratio of the minimum effective dose to the estimated ED_{90} for each chemical was then determined. In future field tests with rainfast chemicals, conversion factors of 4, 8, and 12 times the lab ED_{90} seem appropriate. Increasing the factors to 5, 10, and 15 should suffice to assure comparable effects for chemicals adversely affected by rain.

Literature Cited

Gillette, N.L.; Robertson, J.L.; Lyon, R.L. 1978. Bioassays of TH6038 and difluron applied to western spruce budworm. J. Econ. Entomol. 71:319-322.

Granett, J.; Retnakaran, A. 1977. Stadial susceptibility of eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera:Tortricidae) to the insect growth regulator Dimilin®. Can. Entomol. 109:893-894.

Haverty, M.I., Robertson, J.L. 1982. Laboratory bioassays for selecting candidate insecticides and application rates for field tests on the western spruce budworm. J. Econ. Entomol. 75:179-182.

Robertson, J.L.; Boelter, L.M. 1979a. Toxicity of insecticides to Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera:Lymantriidae). I. Contact and feeding toxicity. Can. Entomol. 111:1145-1159.

Robertson, J.L.; Boelter, L.M. 1979b. Toxicity of insecticides to Douglas-fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera:Lymantriidae). II. Residual toxicity and rainfastness. Can. Entomol. 111:1161-1175.

Robertson, J.L.: Haverty, M.I. 1981. Multiphase laboratory bioassays to select chemicals for field testing on the western spruce budworm. J. Econ. Entomol. 74:148-153.

Williams, C.B. 1973. Field tests of four insecticides against the Douglas-fir tussock moth in Oregon. Pages 77-83 *in* Perm Assoc. Comm. Proc., West Forest Conservation Assoc., Portland, OR. 182 p.

Discussion Group A —
Chemicals

Predicting Response of Western Spruce Budworm to Insecticides

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Recognition of the ubiquity and importance of population variation, increased sophistication of insecticide bioassay procedures, and computerized data-processing are permitting us to predict with greater accuracy the results of insecticide application to western spruce budworm in the field. Not long ago, forest entomologists assumed that any chemical toxic to one population within a species would be equally toxic to other populations of that species. However, comparisons of response between laboratory and field populations and among sibling groups of western spruce budworm suggested that a three-fold difference in response was to be expected among previously untreated populations, and that these differences in response have a genetic basis (Stock and Robertson 1980). Subsequent studies showed that response among populations previously treated with insecticides varies much more — as much as 18-fold in some cases (Robertson and Stock 1985).

Electrophoretic analysis of insect esterases (enzymes involved in insecticide metabolism) has shown that specific genotypes are directly linked to insecticide susceptibility (e.g., Beranek 1974; Sudderuddin 1973). Using a combination of genetic and toxicological analyses, we have been able to characterize western spruce budworm populations as inherently susceptible, tolerant, or resistant to two commonly used chemicals, acephate (Orthene®) and carbaryl (Sevin®-4-oil). In addition, laboratory bioassays have provided information on the ways that other biological characteristics (such as developmental stage) and environmental factors (such as surrounding foliage and moisture conditions) can affect relative toxicity of insecticides applied in the field.

A probability model was developed to integrate information on variables known to affect insecticide efficacy in field applications and to simulate their cumulative effects (Force et al. 1982). The model incorporates information on insecticide dose, genetic tolerance level and developmental stage of the insects, and foliage moisture conditions. Model results suggest, for example, that for acephate-tolerant western spruce budworm (the most common population type), low doses are nearly as effective as high doses during the fifth week after emergence (Figure 1). When western spruce budworms are sprayed with carbaryl, predicted mortality falls steadily as larvae age, regardless of dose (Figure 2). As expected, predicted mortality is very low if the foliage is wet at the time of spraying or if rain is expected soon after spray application.

The model can help us provide after-the-fact explanation of why successful or unsuccessful results were obtained by a chemical control effort and, perhaps more important, can permit more accurate forecasts of insecticide efficacy. The original computer program has now been developed and expanded to simulate efficacy of any chemical over time during seasonal

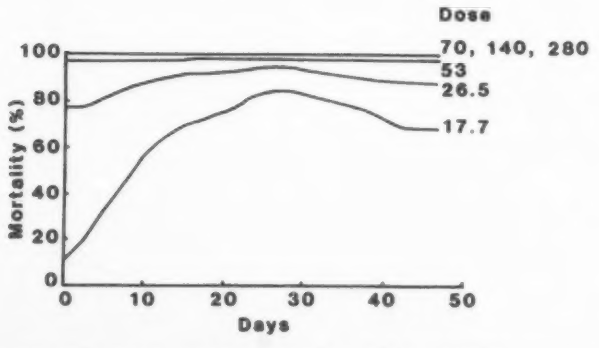

Figure 1. Simulated mortality of acephate-tolerant western spruce budworm treated with one of 6 doses of acephate on any day after emergence of second-stage larvae from hibernaculae.

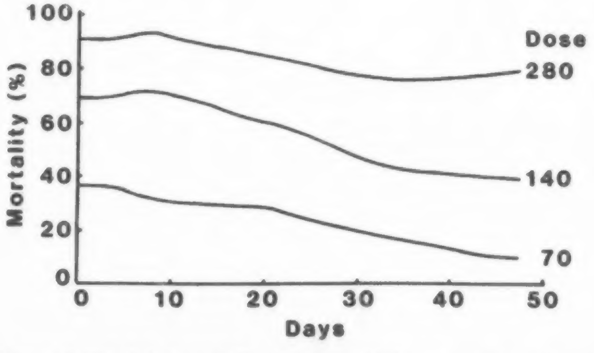

Figure 2. Simulated mortality of carbaryl-tolerant western spruce budworm treated with one of 3 doses of carbaryl on any day after emergence of second stage larvae from hibernaculae.

development of western spruce budworm and other forest defoliators. This second-stage program will permit comparison of the efficacy of a diversity of chemicals when decisions are being made in a control program.

Information obtained with models such as these will enable forest managers to use chemical control more judiciously, choosing to use it when it will be most effective, choosing alternative methods when model output suggests that chemical control will be ineffective. Ultimately, time and effort can be saved, and environmental contamination by toxic chemicals reduced.

Literature Cited

Beranek, A.P. 1974. Esterase variation and organophosphate resistance in populations of *Aphis fabae* and *Myzus persicae*. Entomol. Exp. Appl. 17:129-142.

Force, J.E.; Robertson, J.L.; Stock, M.W.; Williams, C.B. 1982. Probability model of insecticide efficacy for western spruce budworm (Lepidoptera:Tortricidae) and Douglas-fir tussock moth (Lepidoptera:-Lymantriidae). Environ. Entomol. 11:1170-1177.

Robertson, J.L.; Stock, M.W. 1985. Toxicological and electrophoretic population characteristics of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera:Tortricidae) populations. Can. Entomol. 117:57-65.

Stock, M.W.; Robertson, J.L. 1980. Inter- and intraspecific variation in selected *Choristoneura* species (Lepidoptera:Tortricidae): a toxicological and genetic survey. Can. Entomol. 112:1019-1027.

Sudderuddin, K.I. 1973. An electrophoretic study of some hydrolases from an OP-susceptible and an OP-resistant strain of the green peach aphid, *Myzus persicae* (Sulz.). Comp. Biochem. Physiol. 44B:923-929.

Discussion Group A — Chemicals

Research on Chemical Insecticides for Spruce Budworm Control at the Forest Pest Management Institute, 1982 – Present

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Since 1982, research scientists in the Chemical Control Agents Program have been involved primarily with the development and evaluation of new formulations and tank mixes of insecticides currently used for spruce budworm control in Canada. Some of the recent highlights of this program include:

1. The temporary registration of a new, flowable formulation of aminocarb, Matacil® 180F in 1982 following extensive investigations by FPMI scientists over 3 years.
2. The evaluation of a new, commercial formulation of fenitrothion, Sumithion® 20 Flowable which can be mixed directly with water. The physical and chemical characteristics of the latest version of this formulation are acceptable, its toxicity to spruce budworm larvae is comparable to other aqueous formulations of fenitrothion and it was subjected to field tests in small 50-ha (124-acre) blocks during 1984.
3. The development of new aqueous tank mixes of fenitrothion and aminocarb using the emulsifiers Triton X100 and Triton X114. Triton X100 mixes were found to be too viscous at low temperatures but the physical and chemical properties of Triton X114 mixes were suitable and their toxicity to spruce budworm larvae in the laboratory was comparable to standard aqueous mixes of these insecticides. These mixes recently underwent operational testing in the New Brunswick spruce budworm control program.
4. The evaluation of new formulations of Zectran® from Union Carbide. This carbamate insecticide was previously registered in Canada for forestry use by Dow Chemical Co. but this registration lapsed. Union Carbide has acquired the rights to Zectran® and are interested in registering it for this purpose again. The physical, chemical, and spray characteristics of the current liquid formulation are suitable when mixed either directly with oil or with water plus an emulsifier. Its toxicity by several methods of exposure to spruce budworm larvae in the laboratory is similar to comparable formulations of aminocarb and the efficacy of this formulation was assessed by aerial application to small 50-ha (124-acre) blocks in 1984.
5. The evaluation of two new insecticides, Larvin® and AC 217-300 in the laboratory to assess their potential for the control of spruce budworm larvae. Larvin® or thiodicarb is an oxime carbamate insecticide from Union Carbide. On treated foliage its toxicity is comparable to aminocarb and its longevity is very good under natural weathering conditions. AC 217-300 is a novel amidinohydrazone insecticide developed by American Cyanamid Co. It is an odorless, slow-acting, stomach insecticide and is generally inactive by contact. On treated host foliage, it is very potent to spruce budworm larvae with mortality occurring slowly. We are presently investigating how quickly feeding ceases after exposure to this insecticide.

In the immediate future, scientists at the Forest Pest Management Institute will continue development of Sumithion® 20 Flowable and Zectran® towards registration, depending on the results of the 1984 field trials with these products. The results with Larvin® and AC 217-300 to date suggest that these new insecticides warrant further investigation. Regarding other chemical insecticides, only a few new compounds are currently being introduced for development by the chemical industry, primarily for agricultural use. Future insecticides for spruce budworm control will almost certainly have to be registered for major agricultural uses before being considered for forestry because the latter is a relatively small market. Only a portion of those few insecticides which eventually receive such a registration are likely to be acceptable in terms of effectiveness, cost, and environmental impact for spruce budworm control. Consequently, I anticipate only a trickle of new insecticides for evaluation and very few of these will likely reach registration.

There does seem to be a trend within the chemical industry towards the development of new types of insecticides differing in their mode of action from the conventional organophosphorous, carbamate, and organochlorine insecticides. Perhaps we will see some exciting new insecticides in the future. I believe we will see progressive refinement of the current insecticides to enhance their effectiveness, reduce application costs, and increase their safety further through improvements to formulations and application technology. Lower dosages and volumes could result from improvements that increase deposit at the target site and produce a large proportion of optimum size droplets. The development of new formulations specifically designed to be sprayed without diluents at ultra-low-volumes would also be a significant advance in the efficient use of chemical insecticides for spruce budworm control.

Discussion Group A —
Chemicals

Budworm Management in Montana

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For this presentation I have divided budworm management activities in Montana into three periods. The earliest period (1948-1966) is characterized by large scale operational DDT suppression projects (Johnson and Denton 1975). During the second period (1967-1976) much controversy arose over DDT, and included the withdrawal of DDT from forest use. This period ended with the preparation of an environmental statement (U.S. Forest Service 1977) in Region 1. There were no operational projects during this time. From 1977 to the present was the second period with no budworm suppression programs on national forest lands. Of greatest importance was an accelerated research and development program (CANUSA). This period will be considered closed when pest managers finish a current review and evaluation of budworm-caused impacts in the region.

Western spruce budworm activity and damage have occurred throughout most of the Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and true fir (*Abies* spp.) stands in Montana during the past three decades. Areas of aerially visible budworm defoliation have been recorded annually since 1948 (Table 1) and it is from this record that budworm management must be viewed.

1948-1966

The first operational budworm suppression project in Montana was on the Helena National Forest in 1952. DDT was sprayed on 47 406 ha (117,140 acres). Many more DDT projects followed and by 1964 over 1.2 million ha (3 million acres) had been treated. Operational use of DDT ended in 1963 when 167 996 ha (415,120 acres) were sprayed. Table 2 gives the area treated with DDT during this 11-year period.

The last operational suppression project in Montana on national forest land was in 1966. This project was the first and last operational use of a non-DDT product for budworm control. Malathion was sprayed on 33 602 ha (83,030 acres).

1967-1976

Although no operational projects were conducted, deep concern arose over the widespread use of DDT which had ended only a few years before. As public concern increased, managers saw a need for alternate materials. Many years were devoted to laboratory and field testing of other pesticides, and the development of ultra low-volume application technology. The Environmental Protection Agency ruled in 1972 that DDT could no longer be used in forestry without special approval. In response to the continuing high levels of budworm

Table 1
Budworm defoliation in Montana from 1948 to 1983*

Year	*Defoliation*	
	(Ha)	*(acres)*
1948	*105 851*	*261,560*
1949	*164,306*	*406,000*
1950	*276 811*	*684,000*
1951	*461 999*	*1,141,600*
1952	*665 564*	*1,644,610*
1953	*744 354*	*1,839,300*
1954	*786 183*	*1,942,660*
1955	*1 299 259*	*3,210,470*
1956	*1 681 011*	*4,153,780*
1957	*1 775 017*	*4,386,068*
1958	*1 867 129*	*4,613,678*
1959	*1 871 388*	*4,624,201*
1960	*1 028 183*	*2,540,642*
1961	*1 140 388*	*2,817,900*
1962	*1 171 562*	*2,894,930*
1963	*810 182*	*2,001,960*
1964	*816 074*	*2,016,520*
1965	*1 110 412*	*2,743,830*
1966	*695 323*	*1,718,145*
1967	*725 617*	*1,793,000*
1968	*1 222 108*	*3,019,830*
1969	*1 092 488*	*2,699,540*
1970	*819 461*	*2,024,890*
1971	*1 026 021*	*2,535,300*
1972	*1 157 298*	*2,859,685*
1973	*667 009*	*1,648,180*
1974	*890 830*	*2,201,242*
1975	*1 241 383*	*3,067,458*
1976	*1 056 594*	*2,610,846*
1977	*1 235 959*	*3,054,055*
1978	*1 011 786*	*2,500,125*
1979	*919 231*	*2,271,422*
1980	*394 638*	*975,152*
1981	*377 156*	*931,953*
1982	*913 116*	*2,256,311*
1983	*1 057 638*	*2,613,425*

*Includes the Idaho portion of the Bitterroot National Forest.

Table 2
Area treated with DDT in Montana from 1953 to 1963

Year	Defoliation (Ha)	Defoliation (acres)	Year	Defoliation (Ha)	Defoliation (acres)
1953	47 405	117,140	1959	51 347	126,880
1954	—		1960	47 693	117,850
1955	122 193	301,940	1961	—	
1956	309 947	765,880	1962	181 610	448,760
1957	317 555	784,680	1963	167 996	415,120
1958	—				
Total				1 245 746	3,078,250

infestation during the early 1970s (Table 1) Region 1 initiated a region-wide analysis. An environmental statement outlining budworm management was issued in June 1977 (USDA Forest Service 1977). This document defined how budworm management would be addressed on 1 010 228 ha (2,496,274 acres) of national forest land. The no-action alternative was selected on 824 392 ha (2,037,073 acres) while 185 836 ha (459,201 acres) were proposed for special silvicultural treatment. Implementation of the silvicultural alternative has been slow and good examples are few. Direct suppression with pesticides was retained for optional use by two National Forests and rejected by the others. However, no operational spraying has been done.

1977-Present

When CANUSA began in 1977, Region 1 recommended they were not to finance any further work on chemical pesticides for large scale operational control programs. Within the Region our efforts focused on developing individual tree treatments using implants, injections, and ground sprays for foliage and cone protection. We also conducted a *Bacillus thuringiensis* (B.t.) pilot control project and 2-year followup evaluation. The western component of CANUSA focused its efforts on developing a decision-support system. This computer-based system will give land managers a tool that will provide growth and yield projections based on both insect and stand data. This and other improved techniques in sampling and evaluations procedures will enable land managers to better analyze and interpret budworm impacts. In February 1984 Region 1 began its second region-wide evaluation of the budworm situation in Montana and Idaho. This review will be used to update or amend the 1977 document.

Literature Cited

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of the western spruce budworm in the American Northern Rocky Mountain area from 1922 through 1971. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn, Ogden, UT. Gen. Tech. Rep. INT-20.

USDA Forest Service. 1977. Final environment statement, western spruce budworm management plan, June 1977. U.S. Dep. Agric., For. Serv., Region 1, Missoula, MT. 389 p.

Discussion Group A — Chemicals

Spraying for Control of the Western Spruce Budworm in the Pacific Northwest

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The Pacific Northwest encompasses the States of Oregon and Washington and a small part of northern California. The Region includes over 21.5 million ha (53 million acres) of forested land of which 2.8 million ha (7 million acres) is in the mixed-conifer type — host of the western spruce budworm (*Choristoneura occidentalis* Freeman). The western spruce budworm was first recorded in 1914 from Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) collected in southern Oregon.[1] Small outbreaks were recorded in central Washington and in central Oregon in 1929 (Dolph 1980). Larger outbreaks occurred in central Washington and northeastern Oregon in the 1940s, defoliating 1.2 million ha (3 million acres) in 1950. The current outbreak in northeastern Oregon was first detected in 1980 and increased to 971 280 ha (2.4 million acres) in 1983.[2]

Aerial spraying for budworm control in the Pacific Northwest began with an experimental trial of DDT in 1948 (Dolph 1980). Operational spraying was initiated in 1949. Yearly projects have ranged from 13 760 ha (34,000 acres) in 1979 to 377 585 ha (933,000 acres) in 1950 (Dolph 1980). From 1948 to 1983, 2.5 million ha (6.2 million acres) have been sprayed. Only three materials, DDT, Malathion, and carbaryl have been used on an operational basis. Acephate was used near critical anadromous fish streams in 1982. Toxaphene, dieldrin, fenitrothion, Matacil®, mexacarbate, and *Bacillus thuringiensis* have been tested but not used operationally. Cost of treatment has ranged from $1.70 to $22.67 per ha ($0.69 to $9.18 per acre).

Both fixed- and rotary-winged aircraft have been used to apply the insecticides. In 1949, 13 Stearman aircraft and 3 Bell helicopters were used.[3] Other early projects used single- and multi-engine fixed-wing and rotary-wing aircraft.[1,4,5,6,7] As many as 85 single-engine, 8 multi-engine, and 25 standby spray planes were used on a single project.[8] Helicopters have been employed almost exclusively since 1976.

The continuing objective of spraying in the Pacific Northwest has been to reduce budworm populations to a point where resurgence will not occur during the existing outbreak. This has usually been accomplished with a single application in late instars. Larval mortality with DDT averaged between 96.2 and 99.2 percent, with malathion 84.3 percent, and with carbaryl 91.7 to 96.2 percent. The key measure of spray effectiveness is larval survival and has been measured since 1982. In 1983, the target of 1.5 or less larvae per 45 cm branch tip was obtained with carbaryl on about 80 percent of the units treated. During the history of treatment in the Pacific Northwest, few units have needed retreatment during the same outbreak. Over large areas, spraying remains the only viable alternative for reducing losses caused by the western spruce budworm.

Literature Cited

Dolph, R.E. 1980. Budworm activity in Oregon and Washington — 1947-1979. U.S. Dept. Agric., For. Serv., Pac. Northwest For. Region, Portland, OR. 54 p.

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[1] Lindsten, A.; Buckhorn, W.J.; Wear, J.F.; Whiteside, J.M.; Wright, K.H. 1949. Spruce budworm situation in Oregon and Washington — 1949 season. U.S. Dept. Agr. BUR. Ent. and Plant Quar. Report. Portland, OR. 27 pp. and Appendix. Sept. 1, 1949.

[2] USDA Forest Service. 1984. Environmental assessment — western spruce budworm management in northeastern Oregon. 68 p. and appendices (processed). February 1984.

[3] Lindsten, A.; Wright, K.H. 1951. Report on the 1949 western Oregon spruce budworm control project. Oregon State Board of Forestry and USDA Bureau of Entomology and Plan Quarantine Report. 71 pp. (processed). March 30, 1951.

[4] Woods, J.B. Jr.; Lindsten, A.; Larsen, A.T. 1951. The 1950 spruce budworm control project. Oregon State Board of Forestry. 30 pp. and appendix (processed). March 1951.

[5] Woods, J.B. Jr.; Compton, L.M.; Larsen, A.T.; McComb, D.P.; Lindsten, A.C. 1954^{a}. The 1952 spruce budworm control project. Oregon State Board of Forestry. 29 pp. (processed). January 1954.

[6] Woods, J.B. Jr.; Compton, L.M.; McComb, D.P.; Larsen, A.T. 1954^{b}. The 1953 spruce budworm control project. Oregon State Board of Forestry. 31 pp. (processed). January 1954.

[7] Woods, J.B. Jr.; Compton, L.M.; McComb, D.P.; Larsen, A.T. 1954^{c}. The 1954 spruce budworm control project. Oregon State Board of Forestry. 37 pp. (processed). December 1954.

[8] Whiteside, J.M. 1956. Spruce budworm control in Oregon and Washington, 1949-1956. U.S. Dep. Agric., For. Serv. PNW Forest and Range Experiment Station, Portland, OR. 23 pp. and illustrations. November 1956.

Discussion Group A — Chemicals

History of Chemical Treatment of the Western Spruce Budworm in Idaho

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The western spruce budworm, *Choristoneura occidentalis* Freeman, is the most widely distributed and destructive defoliating insect of western forests. The first known outbreak of the spruce budworm in the western states was recorded in 1922 after epidemic populations were found causing severe defoliation near Priest Lake in northern Idaho.[1] It had also been found throughout other areas of northern Idaho, and had been recorded on the Payette and Little Salmon River watersheds of southwestern Idaho.

Western spruce budworm epidemics have continued since that time (Johnson and Denton 1975) and the first use of chemicals against the budworm in Idaho took place in 1953. DDT was used operationally at 1121 g/ha (1 lb./acre), applied aerially, over 6 506 ha (16,070 acres) of the Nezperce National Forest just north of the Salmon River (Johnson and Denton 1975). The same year very limited spot spraying was conducted in four areas of southern Idaho with operations based at McCall, Cascade, Warm Springs, (32 km [20 air miles] west of Stanley), and Salmon. In 1955 the first large scale project in southern Idaho was conducted in these same areas (Furniss 1957). Table 1 shows the sequence of all western spruce budworm chemical treatment projects in Idaho, both operational and experimental, from 1953 through 1982.

For the projects conducted from 1953 through 1957, large aircraft were used, spraying long cross-country patterns, disregarding water and topography. Control objectives were to reduce budworm populations to endemic levels or to a level where danger of heavy mortality to trees was alleviated (Johnson and Denton 1975).

In the early 1960s, potential adverse effects of DDT and related chemicals stimulated an aggressive program for development of safer application techniques and for alternative chemicals. The 1963 experimental work on the Salmon NF was the first western project not to treat water areas, deleting a 305-m (1000-ft) buffer on each side of streams or lakes and treating a second 305-m (1000-ft) strip by helicopter, thus making every effort to keep the pesticide out of the water.[2] The 1963 experimental projects on the Targhee NF tested carbaryl and were conducted concurrently with similar projects in Montana testing other compounds as potential replacements for DDT (Johnson and Denton 1975). The 1963 operational project on the Targhee NF was apparently the first in Idaho to use observation aircraft to help the spray planes in their orientation.[3]

The 1964 Salmon NF operational project was of significance in several ways; It was the last project to use DDT against the budworm and it was the first in the west to operationally leave nontreated buffer strips along designated streams and lakes following the pattern tested in 1963. The 1964 Salmon NF project also had the distinction of having Rachael Carson and her observation team present to observe and film the operation.[4] Furthermore, there was an extensive project of monitoring streams for pesticides and their possible effect on fish and aquatic invertebrates.

Other efforts in 1964 and several subsequent years were on an experimental basis testing potential replacements for DDT. Chemicals that eventually were registered included Malathion, mexacarbate, and carbaryl.

The 1967 Sawtooth NF experimental project was of special interest, being planned for use of 13.6 g (0.03 lb) of Zectran in one-half pint carrier per acre. The spray design was to take advantage of atmospheric transport and diffusion by using a fine mist spray with droplets of less than 50 microns (D-max 50, mass median diameter [mmd] of 20 microns or less). The decision to use droplets of this small size was based on 1966 work where a fluorescent dye was added to the spray and used to determine what size drop was most effective in hitting the insect. To obtain this small droplet size, a spray system was designed utilizing freon as a dispersant. The freon and formulated insecticide were maintained in two separate systems with mixing and discharge occurring in a special bi-fluid nozzle. Although the desired 50 micron size was not achieved (field measurements showed mmd's of 70-80 microns with a D-max over 120 microns), it was believed that these were the smallest droplet sizes produced by any practical aerial spray system at that time (Taynton 1968). A neodymium lidar gun, which transmitted a beam combining radar and laser, was also used on this project to track and quantify the dispersal and deposit of spray materials (Taynton 1968).

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[1] Spruce budworm in northern Idaho. 1922. James C. Evenden, Entomologist in Charge, Northern Rocky Mountain Field Station, Coeur d'Alene, Idaho. Unpublished Research Report. USDA, Bureau of Entomology and Plant Quarantine. Forest Insect Investigations.

[2] Personal Communication, Gerald Wilson, Application Contractor, Hillcrest Aircraft Co., Lewiston, ID.

[3] Personal Communication, Lorris Benedick, Area Supervisor, Idaho Dept. of Lands, Idaho Falls, ID.

[4] Personal Communication, Gerald Wilson, Application Contractor, Hillcrest Aircraft Co., Lewiston, ID.

Table 1

Operational and experimental aerial spray projects for control of the western spruce budworm in Idaho, 1953-1979 (Adapted from Johnson and Denton 1975)

			Insecticide used		
Year	Adjacent state & private lands	Type of treatment	Toxicant	Toxicant/acre	Acreage or trees treated (Reference)
1953	Nezperce N.F.	Operational	DDT	1.0 lb.	16,070[1]
	Boise N.F.	Operational?	DDT	1.0 lb	spot treatment[2]
	Payette N.F.	Operational?	DDT	1.0 lb.	spot treatment[2]
	Salmon N.F.	Operational?	DDT	1.0 lb	spot treatment[2]
1954	Boise N.F.	Operational	DDT	1.0 lb.	spot treatment[2,3]
	Payette N.F.	Operational	DDT	1.0 lb.	spot treatment[2,3]
	Salmon N.F.	Operational	DDT	1.0 lb.	spot treatment[2,3]
1955	Nezperce N.F.	Operational	DDT	1.0 lb.	70,710[1]
	Boise N.F.	Operational	DDT	1.0 lb.	621,210[1]
	Payette N.F.	Operational	DDT	1.0 lb.	216,000[1]
	Salmon N.F.	Operational	DDT	1.0 lb.	small acreage[2]
1956	Boise N.F.	Operational	DDT	1.0 lb.	211,090[1]
	Challis N.F.	Operational	DDT	1.0 lb.	10,880[1]
	Clearwater N.F.	Operational	DDT	1.0 lb.	119,370[1]
	Payette N.F.	Operational	DDT	1.0 lb.	98,110[1]
	Salmon N.F.	Operational	DDT	1.0 lb.	139,800[1]
	Targhee N.F.	Operational	DDT	1.0 lb.	16,010[1]
1957	Boise N.F.	Operational	DDT	1.0 lb.	92,370[1]
	Challis N.F.	Operational	DDT	1.0 lb.	20,110[1]
	Payette N.F.	Operational	DDT	1.0 lb.	374,180[1]
	Salmon N.F.	Operational	DDT	1.0 lb.	55,610[1]
	Targhee N.F.	Operational	DDT	1.0 lb.	118,360[1]
1963	Salmon N.F.	Experimental	DDT	0.5 lb.	16,500[1]
	Targhee N.F.	Experimental	Carbaryl	1.6 lb.	2,500[1]
		Experimental	Carbaryl	0.8 lb.	2,500[1]
		Operational	DDT	0.0 lb.	
		Operational	DDT	0.5 lb.	190,000[1]
		Operational	DDT	1.0 lb.	
1964	Salmon N.F.	Operational	DDT	0.5 lb.	39,200[1]
		Operational	DDT	1.0 lb.	485,870
		Experimental	Dimethoate	4.0 oz.	1,080
		Experimental	Mexacarbate	1.6 oz.	60[1]
		Experimental	Pyrethrins	0.01 lb.	60[1]
		Experimental	Dichlorovos	0.1 lb.	20[1]
1965	Salmon N.F.	Experimental	Malathion	13.0 fl. oz.	4,200[1]
				9.0 fl. oz.	3,950[1]
1966	Salmon N.F.	Experimental	Mexacarbate	2.4 oz.	4,860[1]
1967	Sawtooth N.F.	Experimental	Mexacarbate	2.4 oz.	2,300[1]
1969	Nezperce N.F.	Experimental	Mexacarbate	2.4 oz.	6,000[1]
1971	Nezperce N.F.	Experimental	Mexacarbate	2.4 oz.	9,000[1]

Table 1 (concluded)

1976	*Targhee N.F.*	*Experimental*	*Acephate*	*1.0 lb.*	*300*[4]
	Targhee N.F.	*Experimental*	*Acephate*	*0.5 lb.*	*300*[4]
	Targhee N.F.	*Experimental*	*Acephate*	*0.25 lb.*	*300*[4]
	Targhee N.F.	*Experimental*	*Methomyl*	*1.0 lb.*	*150*[5]
	Targhee N.F.	*Experimental*	*Methomyl*	*0.5 lb.*	*150*[5]
	Targhee N.F.	*Experimental*	*Methomyl*	*0.25 lb.*	*150*[5]
1977	*Payette N.F.*	*Experimental*	*Chlorpyrifos-methyl*	*8.0 oz.*	*225*[6]
	Payette N.F.	*Experimental*	*Chlorpyrifos-methyl*	*4.0 oz.*	*225*[6]
	Payette N.F.	*Experimental*	*Chlorpyrifos-methyl*	*2.0 oz.*	*225*[6]
	Payette N.F.	*Experimental*	*Acephate*	*0.5 lb.*	*4,000*[7]
1978	*Boise N.F.*	*Experimental*	*Methomyl*	*8.0 oz.*	*200*[8]
	Boise N.F.	*Experimental*	*Methomyl*	*4.0 oz.*	*200*[8]
	Boise N.F.	*Experimental*	*Methomyl*	*2.0 oz.*	*200*[8]
	Boise N.F.	*Experimental*	*Acephate*	*medicap implants*	*24 trees*[9]
1979	*Boise/Payette N.F.*	*Operational*	*Acephate* *Carbaryl*	*0.5 lb.* *1.0 lb.*	*47,260*[10] *92,270*[10]
	Payette N.F.	*Experimental*	*Acephate*	*medicap implants*	*120 trees*[11]
1980	*Payette N.F.*	*Experimental*	*Acephate*	*medicap implants*	*½ of 1979 trees*[12] *2nd treatment*
	Payette N.F.	*Experimental*	*Sulprofos*	*8.0 oz.*	*40*[13]
	Payette N.F.	*Experimental*	*Sulprofos*	*4.0 oz.*	*40*[13]
	Payette N.F.	*Experimental*	*Sulprofos*	*2.0 oz.*	*40*[13]
	Payette N.F.	*Experimental*	*Phosmet*	*1.5 lb.*	*40*[13]
	Payette N.F.	*Experimental*	*Phosmet*	*1.0 lb.*	*40*[13]
	Payette N.F.	*Experimental*	*Phosmet*	*8.0 oz.*	*40*[13]
	Payette N.F.	*Experimental*	*SIR-8514*	*4.0 oz.*	*150*[14]
	Payette N.F.	*Experimental*	*Acephate*	*glass cartridge*	*20 trees*[15]
1981	*Payette N.F.*	*Experimental*	*Acephate*	*glass cartridge*	*¼ of 1980 trees*[15]*)*
	Payette N.F.	*Experimental*	*Acephate*	*medicap implants*	*5 trees*[15]
	Payette N.F.	*Experimental*	*Carbofuran*	*medicap implants*	*5 trees*[15]
	Payette N.F.	*Experimental*	*Dimethoate*	*medicap implants*	*5 trees*[15]
	Payette N.F.	*Experimental*	*Oxydemeton-methyl*	*Mauget injector*	*5 trees*[15]
	Payette N.F.	*Experimental*	*Meth-amidophos*	*glass cartridge*	*5 trees*[15]
1982	*Payette N.F.*	*Experimental*	*Acephate*	*medicap implants*	*10 trees*[16]
	Payette N.F.	*Experimental*	*Bendiocarb*	*medicap implants*	*10 trees*[16]
	Payette N.F.	*Experimental*	*Oxydemeton-methyl*	*Mauget injector*	*20 trees*[16]
	Boise N.F.	*Experimental*	*Acephate*	*medicap implants*	*10 trees*[16]
	Boise N.F.	*Experimental*	*Bendiocarb*	*medicap implants*	*10 trees*[16]
	Boise N.F.	*Experimental*	*Oxydemeton-methyl*	*Mauget injector*	*20 trees*[16]

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[1] Johnson, P.C.; Denton, R.E. 1975.

[2] Personal communication, Gerald Wilson, Application Contractor, Hillcrest Aircraft Co., Lewiston, ID.

[3] Taynton, Shag (Roger). 1967.

[4] Markin, G.P. 1979b.

[5] Markin, G.P. 1977.

[6] Markin, G.P.; Grimble, D.G. 1978.

[7] Stipe, L.E.; Knopf, J.A.E.; Livingston, R.L.; Markin, G.P.; Young, R.W. 1977.

[8] Markin, G.P. 1979a.

[9] Markin, G.P. 1979c.

[10] Livingston, R.L.; Schwandt, J.W.; Preson, J.; Ciesla, W.; Davidek, B.; Beckman, D.; Spicklemire, L.; Johnson, R. 1982.

[11] Reardon, R.C.; Haskett, M.J. 1981.

[12] Reardon, R.C. 1984.

[13] Markin, G.P.; Johnson, D.R. 1981.

[14] Johnson, D.R.; Markin, G.P. 1981.

[15] Reardon, R.C.; Barrett, L. 1984.

[16] Reardon, R.C.; Cahill, D.; Thier, R.W. 1984.

The most recent work in Idaho included the completion of a pilot control project testing acephate (Stipe et al. 1978), and an operational project utilizing both carbaryl and acephate (Livingston et al. 1982). Experimental work included tests of capsules implanted into xylem tissue for pesticide transport to the foliage and cones and small field experiments testing acephate, methomyl, chlorpyrifos-methyl, phosmet, sulprofos and SIR-8514, a moulting inhibitor. Of special interest is the 1982 work testing systemic chemical insecticides as means of increasing seed yield in Douglas-fir.

Literature Cited

Furniss, M.M. 1957. Entomological Aspects of the 1955 Spruce Budworm Control Project in Southern Idaho. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn, Ogden, UT. Misc. Pub. No. 10. 22 p.

Johnson, D.R.; Markin, G.P. 1981. Western spruce budworm aerial application with SIR-8514, 1979-1980. Insecticide and Acaracide Tests 6:158(279).

Johnson, P.C.; Denton, R.E. 1975. Outbreaks of the western spruce budworm in the American Northern Rocky Mountain Area from 1922 through 1971. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn, Ogden, UT 84401. Gen. Tech. Report INT-20, 144 p.

Livingston, R.L.; Schwandt, J.W.; Preston, J.; Ciesla, W.; Davidek, B.; Beckman, D.; Spicklemire, L.; Johnson, R. 1982. 1979 Western Spruce Budworm Control Project, Cascade, ID. Forest Insect & Disease Section, Idaho Dept. of Lands, P.O. Box 670, Coeur d'Alene, ID 83814. Report No. 82-4, 64 p.

Markin, G.P. 1977. Field test of two candidate insecticides, Orthene and Lannate, against the western spruce budworm in the Targhee National Forest, 1976. USDA Forest Service Progress Report. U.S. Dep. Agric., For. Serv., Pacific Southwest For. and Range Exp. Stn, Davis, CA.

Markin, G.P.; Grimble, D.G. 1978. Field test of the insecticide Reldan against the western spruce budworm in the Payette National Forest, Idaho, 1977. U.S. Dep. Agric., For. Serv., Pacific Southwest For. and Range Exp. Stn, Davis, CA. Final Report.

Markin, G.P. 1979a. Western spruce budworm control with Lannate, 1978. Insecticide and Acaracide Tests 4:176(273).

Markin, G.P. 1979b. Effects of acephate sprayed on western spruce budworm in Idaho, 1976. J. Econ. Entomol. 72:414-415.

Markin, G.P. 1979c. Western spruce budworm control with orthene implants, 1978. Insect. and Acar. Tests 4:175(270).

Markin, G.P.; Johnson, D.R. 1981. Western spruce budworm aerial field Tests, 1980. Insecticide and Acaracide Tests 6:159(280).

Reardon, R.C. 1984. Two consecutive yearly applications of Orthene medicaps increase protection of grand fir against western spruce budworm. Forest Ecology & Management. 7:183-196.

Reardon, R.C.; Barrett, L. 1984. Reducing western spruce budworm populations on grand fir and Douglas-fir with acephate, carbofuran, dimethoate, oxydemetron-methyl, and methamidophos. Forest Ecology and Management. 8:1-10.

Reardon, R.C.; Haskett, M.J. 1981. Effect of Orthene medicaps on populations of western spruce budworm on grand fir and Douglas-fir. J. Econ. Entomol. 74:266-270.

Reardon, R.C.; Cahill, D.; Thier, R.W. 1984. Implantation and injection of systemic chemical insecticides in Douglas-fir in Idaho to increase seed yield. U.S. Dep. Agric., For. Serv., Forest Pest Management, Intermountain Region, Boise, ID. Report 84-6. 9 p.

Stipe, L.E.; Knopf, J.A.E.; Livingston, R.L.; Markin, G.P.; Young, R.W. 1977. A pilot control project with Orthene for control of the western spruce budworm, McCall, ID, 1977. U.S. Dep. Agric., For. Serv., Forest Pest Management, Intermountain Region, Ogden, UT. Final Report, 34 p.

Taynton, Shag (Roger). 1967. The operational plan for the 1967 Big Smokey Spruce Budworm Project. An administrative study of Zectran vs. spruce budworm. USDA Forest Service Project Plan. Sawtooth National Forest, Twin Falls, ID.

Taynton, Shag (Roger). 1968. The 1967 Big Smokey Spruce Budworm Zectran Project. Sawtooth National Forest, Twin Falls, ID. USDA Forest Service Final Report, 48 p.

Discussion Group A — Chemicals

Spruce Budworm Control Program in Eastern Canada

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The current outbreak of spruce budworm in Eastern Canada extends over an area of 27 540 000 ha (68,051,340 acres) of forest. The forested areas under attack represent not only a significant resource base to the Canadian and provincial economies through the forest industries, but also are of importance to the tourist industry and from an environmental point of view. The management of the forest resource in Canada is a provincial responsibility; thus response to the budworm infestation reflects provincial concerns. The role of the Canadian Forestry Service (CFS) is to carry out research which will aid in the management of the forest resource and the control of pest insects such as the spruce budworm. Thus, although the CFS is not involved in any control program, the CFS research results have led to the introduction of effective, environmentally acceptable insecticides, the development of spray strategies, and the development of guidelines to prevent adverse effects from sprays.

The spray programs that are carried out by each province rely on the use of federally registered insecticides. In Canada the chemical insecticides most commonly used for spruce budworm control are aminocarb (registered as Matacil) and fenitrothion (registered as Sumithion, Folithion and Novathion). The biological or biorational insecticide *Bacillus thuringiensis* (registered as formulations of Dipel, Thuricide, Novabac or Futura) has been used for several years and within the past few years, new developments in its formulation and a better understanding of techniques of application have resulted in increased use. The insecticides acephate (Orthene), carbaryl (Sevin) and trichlorfon (Dylox) have been used in relatively small amounts.

The use of these insecticides and the size of the area being protected indicate provincial concerns about the local forest industry, the forest resource within the province, and the possible effects of spraying on human health and the forest ecosystem. Specifics on the area of infestation, area treated, insecticides used, and plans for 1985 are shown in Table 1. Examination of the table reveals aspects of the provincial programs. The spray program in Newfoundland represents about half the area of infestation. The provincial government is satisfied with aminocarb and most of the area is treated with that compound. The province of Nova Scotia relies solely on *Bacillus thuringiensis* (B.t.); confidence in this insecticide and the need to protect more of the forest resource is indicated in the plans to increase the spray program in 1985. B.t. was selected as the insecticide of choice by Nova Scotia because of a desire not to use chemical insecticides. The forested areas of Prince Edward Island are broken into small patches scattered through the agricultural countryside and spraying is not done. In New Brunswick the forest industry is vital to the provincial economy; this is shown by the treatment of over 50 percent of the infested area. Historically, the

Table 1
Spruce budworm control programs in eastern Canada in 1984

	Area infested		*Area treated*		*Insecticide used*		
Province	*(ha)*	*(acres)*	*(ha)*	*(acres)*	*(% of area)*		*Plans for 1985*
Newfoundland	*55 000*	*135,905*	*26 336*	*65,076*	*aminocarb* *B.t.*	*88%* *12%*	*No forecast*
Nova Scotia	*225 000*	*555,975*	*20 537*	*50,747*	*B.t.*	*100%*	*Increase over 1984*
Prince Edward Island	*60 000*	*148,260*	*0*	*0*	*N.A.*		*None planned*
New Brunswick	*2 200 000*	*5,436,200*	*1 320 000*	*3,261,720*	*fenitrothion* *aminocarb* *B.t.*	*47%* *49%* *4%*	*No change over 1984*
Quebec	*13 000 000*	*32,123,000*	*708 950*	*1,751,815*	*aminocarb* *fenitrothion* *B.t.*	*43%* *11%* *46%*	*Treat 800 000 ha (1,976,800 acres)*
Ontario	*12 000 000*	*29,652,000*	*3 700*	*9,143*	*carbaryl* *aminocarb* *B.t.*	*15%* *85%*	*Treat 8 000 ha (19,768 acres)*

province has used fenitrothion and aminocarb with only small amounts of B.t. Although no change is indicated for 1985, success with B.t. in 1984 may result in a greater proportion of the area being treated with this product. In Quebec, B.t. was used on almost half of the treatment area. A recent ministerial decision from Quebec will mean increased utilization of B.t. with a target of virtually sole use of this material by 1988. Although the province of Ontario has a very large area of forest under attack by the budworm, the area treated is the smallest of any of the programs. This results from the provincial policy to treat only specific areas of high value. It is expected that the program will be increased in 1985.

Although not included in this report the aircraft used also reflect variations in the provincial spray programs. The province of Quebec uses multi-engined aircraft (DC-6, Lockheed Constellation) and ag-type aircraft; New Brunswick has used multi-engined aircraft, TBM Avengers, MI-18's and ag-type aircraft. Ontario, Nova Scotia, and Newfoundland all rely on ag-type spray aircraft including helicopters for specific areas.

Discussion Group A — Chemicals

Summary

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In the beginning there was lead arsenate. Then there was DDT. Then there was Zectran® in the United States and fenitrothion in Canada. Now we have Matacil® and carbaryl.

Where we going now? When do chemicals fit into spruce budworm management? How does a chemical move from the laboratory into the field? These questions were addressed by speakers in this workshop. The first four speakers discussed the use of laboratory data in the selection of both chemicals and their application rates for spruce budworm management, and the development of an insecticide efficacy model. The last four speakers described the various regional use patterns of chemicals in the United States and Canada.

The discussions indicated that the selection of a chemical for operational use to manage spruce budworms is not entirely a scientific process. Rather, the selection process is based on a compromise between science and economics. If a chemical is ultimately used, the manufacturer has chosen to extend a major agricultural registration into the minor market of forestry. In essence, if a chemical is not effective in protecting cotton, soybeans, or another major crop, it will never be available for spruce budworms.

Discussion Group B —
Biorationals

Courtship Disruption of Western Spruce Budworm by Aerial Application of Synthetic Pheromone

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Advantages for using pheromones in pest control include low toxicity, specificity for the target insect, and outstanding environmental safety. For these reasons, we evaluated mating disruption as a control approach for the western spruce budworm (*Choristoneura occidentalis* Freeman).

Procedures

Treatments of 0, 2, 8, 32, and 128 grams/ha (0, 0.03, 0.11, 0.45, and 1.8 oz/acre) pheromone were each applied on two 10-ha (25-acre) plots. The pheromone was formulated in plastic Hercon® flakes (Health Chem. Corp., 10010 Broadway, New York, NY),[1] mixed with an acrylic-base sticker, and dispensed by aircraft. The synthetic pheromone was 88 percent E-11-tetradecenal and 12 percent Z-11-tetradecenal, slightly different than the 92:8 E:Z ratio identified from emissions of female *C. occidentalis* (Cory et al. 1982; Silk et al. 1982). Longevity of the disruption formulation was monitored by collecting flakes from the forest each week and comparing them, by gas chromatographic analysis of pheromone content, to flakes held in a freezer.

The test area in north-central Oregon, forested mainly with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) was lightly defoliated by budworm. Sampling of three 40-cm branches from 10 trees/plot showed uniform budworm abundance in the test area, with larval numbers ranging from two to five per sample set of three branches.

Insect response to treatment was evaluated primarily by captures of adult males in eight sticky traps per plot baited with virgin females. Two traps per plot with PVC plastic baits (Daterman 1974) containing 0.01 percent synthetic pheromone were compared with traps having female lures. All traps were changed weekly. As a further evaluation we caged 15 pairs of moths in 65- × 65-cm (26- × 26-in) cages with foliage, and then determined the production of fertile egg masses. We conducted two of these cage tests per each of 8, 32, and 128g/ha disruption treatments and for the untreated check.

Results and Discussion

Disruption treatments reduced male trap response in proportion to disruptant dosage (Table 1). Even the higher doses, however, did not completely suppress response (Table 1). Results with the 0.01 percent lure, which approximates the release rate of females (Cory et al. 1982, were similar to the results obtained with female lures (Table 1).

Pheromone content of the dispenser formulation declined rapidly during the first week after application. Over one-half of the total pheromone had diffused out of the formulation after the first 7 days, whereas peak adult activity occurred the second and third weeks after the treatment application (Table 2).

Numbers of egg masses produced by caged pairs were lower in two of the treated plots. Caged adults produced averages of 39.5 (±2.5), 40.5 (±8.8), 11.5

Table 1
Disruption of male attraction to natural and synthetic pheromone lures

Trap lure	*Untreated check*	*Disruption treatment g/ha* 2	8	32	128	*Catch/dosage correlation (r)*
	males/trap/week[1] (95% conf. interval)					
Live female	*60 (±7.3)*	*43 (±4.5)*	*31 (±4.0)*	*17 (±4.8)*	*8 (±6.7)*	*.97*
Synthetic[2] pheromone	*52 (±11.1)*	*44 (±6.4)*	*23 (±5.9)*	*18 (±7.6)*	*2 (±9.9)*	*.92*

[1]Numbers represent mean captures from 8 synthetic and 32 female-baited trap observations per disruption treatment for 2 weeks of peak seasonal flight.
[2]0.01% pheromone by weight in 3 mm diam × 5 mm PVC pellet.

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[1] Mention of proprietary products does not necessarily suggest endorsement by the U.S. Department of Agriculture.

Table 2
Percent of original pheromone remaining in disruption formulation (peak budworm flight occurred during weeks 1-3)

	weeks in field					
	1	*2*	*3*	*4*	*5*	*6*
Pheromone remaining in Hercon flakes (%)	*45*	*26*	*16*	*8*	*7*	*5*

(±6.0), and 20.5 (±0.4) egg masses respectively at dosages of 0, 8, 32, and 128g/ha. We consider this only indicative of a trend, however, because of few test replicates and the insects being unnaturally confined in small cages.

It is encouraging that all treatments of pheromone had apparent effects on male behavior, but the fact that trap captures were not totally suppressed by even the highest treatment may mean this approach is limited for western budworm. Partial mating disruption, however, may provide adequate suppression because natural enemies, unaffected by pheromone treatments, should be more effective against the lower populations that remain. A formulation that releases pheromone uniformly over the entire flight period is needed. Further testing over a larger area is desirable to permit evaluation of actual population effects.

Literature Cited

Cory, H.T.; Daterman, G.E.; Daves, G.D., Jr.; Sower, L.L.; Shepherd, R.F.; Sanders, C.J. 1982. Chemistry and field evaluation of the sex pheromone of western spruce budworm, *Choristoneura occidentalis* Freeman. J. Chem. Ecol. 8:339-350.

Daterman, G.E. 1974. Synthetic sex pheromone for detection survey of European pine shoot moth. U.S. Dep. Agric., For. Serv., Pac. Northwest For. and Range Exp. Stn., Portland, OR. Res. Pap. PNW-180.

Silk, P.J.; Wiesner, C.J.; Tan, S. Ah.; Ross, R.J.; Grant, G.G. 1982. Sex pheromone chemistry of the western spruce budworm, *Choristoneura occidentalis* Freeman. J. Chem. Ecol. 8:351-362.

Adaptation of Wax Moth Baculovirus to the Western Spruce Budworm

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An isolate of baculovirus (CfNPV) from the spruce budworm (*Choristoneura fumiferana*) has been adapted to the cabbage looper (*Trichoplusia ni*). The virus was found to be highly virulent for looper larvae after a single passage. Subsequently, the CfNPV was adapted to the greater wax moth (*Galleria mellonella*) (Stairs et al. 1981). As adaptation occurred in one direction, an attempt was made to adapt the nuclear polyhedrosis virus of the wax moth (GmNPV) to the spruce budworm. This paper reports how this was accomplished.

Neonate western budworm larvae (*C. occidentalis*) were fed GmNPV at a food surface contamination rate of 4×10^3 polyhedra per mm^2 (Temperature 24°C). Virus mortality occurred first on day 15 and reached a maximum (80 percent) on day 33 (Table 1). None of the control larvae died by virus. Diseased larvae stopped feeding, died *without* "wilting" and polyhedra developed *only* in the epithelia cells of the foregut and hindgut.

Four diseased, fourth-instar larvae, whose foregut and hindgut epithelia were heavily infected by GmNPV, were macerated in one ml of water. This preparation was applied to food to obtain a surface contamination rate of 2 polyhedra per mm^2 and neonate budworm larvae (48) were allowed to feed on it continuously. As in the first passage, virus mortality occurred first on day 15 but it had reached a maximum on day 17 and almost every cell of the two diseased larvae were packed with polyhedra (Table 2). These two larvae yielded approximately 10^8 polyhedra which were suspended in one ml of water and applied to obtain a food surface contamination rate of 10^3 polyhedra per mm^2. In this experiment virus mortality occurred first on day 4 and reached 100 percent on day 9 (Table 3). All the diseased larvae "wilted" and "melted" at death and were packed with polyhedra.

A comparison of the activity of the passaged virus with that of the unpassaged virus showed the time for 50 percent mortality (LT_{50}) decreased significantly after passage (Figure 1). The LT_{50} for unpassaged virus was 22 days but for the passaged virus it was only 7 days. This very significant difference occurred even though older larvae (second-instar) were used to assay the passaged virus and the dosage was reduced 75 percent. No virus mortality occurred in any of the control larvae.

These data leave little doubt that this virus (GmNPV) became adapted to the budworm. In addition, the passaged virus was highly virulent for early-instar budworm larvae; the LC_{50} was estimated to be between 1 and 100 polyhedra/mm^2 of food surface.

Table 1

Effects of GmNPV on neonate larvae of *C. occidentalis* at a food surface contamination rate of 4×10^3 polyhedra/mm^2

Once passaged GmNPV				*Control*		
Day	*Living*	*Dead*	*(Virus)**	*Living*	*Dead*	*(Virus)*
10	38	10	(0)	36	12	(0)
15	33	15	(5)	36	12	(0)
19	21	27	(15)	36	12	(0)
23	5	43	(31)	—	—	—
33	2	46	(34)	29	19	(0)

*All larvae showed polyhedra development only in the epithelial cells of the foregut and hindgut.

Table 2

Effects of GmNPV passaged once in *Choristoneura occidentalis* on neonate larvae of *C. occidentalis* at a food surface contamination rate of 2 polyhedra/mm^2

Once passaged GmNPV				*Control*		
Day	*Living*	*Dead*	*(Virus)*	*Living*	*Dead*	*(Virus)*
8	37	11	(0)	32	15	(0)
15	36	12	(1)	32	15	(0)
20	22	26	(2)*	30	17	(0)

*Both larvae were heavily infected, wilted and contained many polyhedra.

Table 3

Effects of GmNPV passaged twice in *Choristoneura occidentalis* on second-instar larvae of *C. occidentalis* at a food surface contamination rate of 10^3 polyhedra/mm^2

Twice passaged GmNPV				*Control*		
Day	*Living*	*Dead*	*(Virus)*	*Living*	*Dead*	*(Virus)*
1	50	0	(0)	50	0	(0)
3	48	2	(0)	48	2	(0)
5	44	6	(4)	48	2	(0)
7	21	29	(24)	46	4	(0)
9	0	50	(47)	46	4	(0)

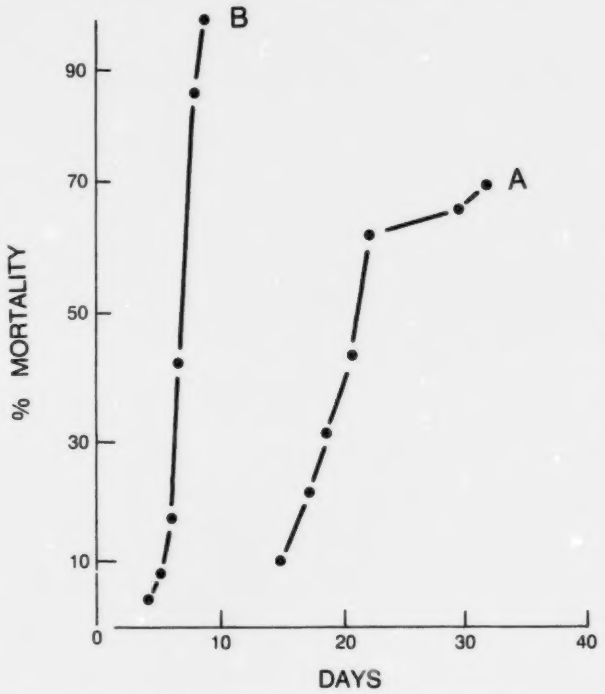

Figure 1. **Comparison of GmNPV (A) with twice-passaged GmNPV (B). The unpassaged virus (A) was fed to neonate *C. occidentalis* larvae at a food surface contamination rate of 4 × 10^3 polyhedra/mm^2 and twice-passaged virus (B) was fed to second-instar larvae at a rate of 10^3 polyhedra/mm^2.**

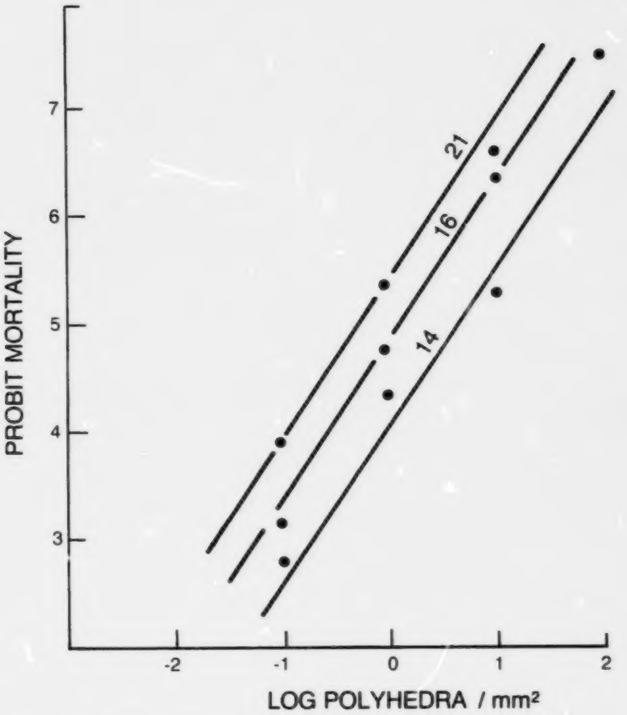

Figure 2. **Dosage-mortality response of second-instar *G. occidentalis* larvae to twice passaged GmNPV. Responses are shown for 14, 16 and 21 days after larvae were placed on virus-contaminated food.**

Furthermore, the yield of polyhedra from diseased larvae appeared to be much above that obtained with the CfNPV and CoNPV isolates.

The activity of the passaged virus was determined more accurately by a dosage-mortality experiment where each of four decimal, serial dilutions (0.1 to 100 polyhedra/mm^2) were fed to 40 second-instar budworm larvae. At 14 days the LC_{50} was 3.16 polyhedra/mm^2, at 16 days it was 1.38 and at 21 days it was 0.20. These results show that the adapted virus was capable of infecting a large fraction of the early larval population at very low dosages, i.e., many larvae were probably infected after consuming only one polyhedron (Figure 2). Possibly, this virus will prove useful in the management of pest populations of budworms.

Literature Cited

Stairs, G.R.; Fraser, T.; Fraser, M. 1981. Changes in growth and virulence of a baculovirus of *Choristoneura fumiferana* after passage in *Trichoplusia ni* and *Galleria mellonella*. J. Invertebrate Pathol. 38:230-235.

Field Persistance and Efficacy of *Bacillus thuringiensis* on Populations of Spruce Budworm in Wisconsin

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To define more precisely some of the inconsistencies in efficacy in the year of treatment and one year posttreatment, two *Bacillus thuringiensis* var. *kurstaki* (HD-1) formulations, Thuricide® 16B and Dipel® 4L, were aerially applied in a single application at a dosage of 20 BIU/ha (8 BIU/acre) and at a volume of 9.35 L/ha (1.0 gal/acre) on spruce budworm (*Choristoneura fumiferana* (Clem.)) populations in Wisconsin (Reardon et al. 1982; Reardon and Haissig 1983).

The experimental area was in northern Wisconsin with a forest type characterized as balsam fir-aspen-paper birch with mature (50 year) balsam fir. In 1980, fifteen 20.2-ha (50-acre) field plots were set out: five replicates of each *B. thuringiensis* formulation and five plots for checks. Balsam fir were used as sample trees. The trees were arranged in 10 three-tree clusters randomly distributed in each plot. Data were collected and recorded by individual tree within each cluster.

All spray was applied the morning of 23 May 1980, with two small fixed-wing aircraft, one for each treatment, equipped with standard spray booms and 8004 Flat Fan tee-jet nozzles. Spray aircraft were calibrated to deliver 9.35 L/ha (1.0 gal/acre) with a droplet volume median diameter (VMD) of 70 μm for Dipel® 4L formulation and 120 μm for Thuricide® 16B.

Primary criteria for spray timing were 90 percent bud cap drop and at least 80 percent third- and fourth-stage larvae. Because of potential impact on the spray coverage, the percentage of hardwood overstory was recorded for each sample tree.

There was no significant difference among pretreatment plot means although significantly greater numbers of spruce budworm larvae/100 buds were found on trees with less than 10 percent overstory and these differences were evident posttreatment. Uncorrected percentage population reduction for treatments was 88 percent for Thuricide® 16B, 85 percent for Dipel® 4L, and 22 percent for checks. Percentage population reduction was corrected by using the ratio of 1- (post – [14 to 16-day]) mean per preplot mean and differences were significant (5 percent level) between the Dipel® and check plots and the Thuricide® and check plots, but not between Dipel® and Thuricide® plots. Average percentage defoliation for each treatment was 52 percent for Thuricide® 16B, 44 percent for Dipel® 4L, and 92 percent for the check plots.

In 1981, 12 of the 15 plots established in 1980 were monitored: 4 plots with each treatment and 4 checks. Within each plot, the 10 three-tree clusters randomly selected in 1980 were resampled. Spruce budworm larval populations were monitored on sample trees at timings that were on the basis of larval development, biologically equivalent to those in 1980. Larvae were categorized as living or dead-moribund, to estimate 1-year posttreatment mortality. Three techniques were used to determine the field presence of *B. thuringiensis*: two culture techniques to detect viable endospores, and an insect bioassay technique to determine total field persistence, i.e., duration of pathogenicity in the field.

Plot means for living larvae were compared for pretreatment and for posttreatment samples; in each case, treatments differed significantly from checks but not from each other. For living larvae, the 1981 percent population reduction did not differ significantly between treatments or between treatments and checks. In 1981, larval development was not delayed in the treated plots, although this was evident in 1980. Average percentage defoliation for each treatment was 6 percent for Thuricide® 16B, 5 percent for Dipel® 4L, and 29 percent for the check plots. Viable endospores of *B. thuringiensis* were recovered on foliage collected 1-year after treatment. The bioassay technique that used larvae from the check plots and foliage from the treated plots indicated that, if viable endospores were present on foliage 1-year posttreatment, the quantities were not sufficient to cause pathogenicity in spruce budworm larvae.

Literature Cited

Reardon, R.C.; Johnson, D.R.; Narog, M.G.; Banash, S.E.; Hubbard, H.B. 1982. Efficacy of two formulations of *Bacillus thuringiensis* on populations of spruce budworm on balsam fir in Wisconsin. J. Econ. Entomol. 75:509-514.

Reardon, R.C.; Haissig, K. 1983. Spruce budworm larval populations and field persistence of *Bacillus thuringiensis* after treatment in Wisconsin. J. Econ. Entomol. 76:1139-1143.

Discussion Group B —
Biorationals

European Parasitoids as Biocontrol Agents of Spruce Budworms

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Spruce budworm outbreaks are natural phenomena associated with the climax phase of the boreal forest succession. Although chemical insecticides are widely used for short-term foliage protection, there is an urgent need to develop more environmentally and socially acceptable long-term strategies for the control of these pests.

Both eastern and western spruce budworms clearly lack an effective entomophage complex (Campbell et al. 1983; McNamee et al. 1981); thus, this component of the defoliating insect/forest system could be manipulated to provide long-term control with minimum disturbance to the forest environment. Such control could be accomplished by augmenting native entomophages or by introducing exotic species, for example, from Europe.

In accordance with this strategy, parasitoids of both western and European origin were released in eastern Canada and the eastern United States during the last major outbreak of *Choristoneura fumiferana* in the late 1940s and early 1950s (Clausen 1978). Unfortunately, these introductions of exotic parasitoids were unsuccessful and typical of the haphazard approach to biocontrol in earlier years. Candidate species were not prescreened for suitability, releases were probably not suitably timed or located, too few individuals were released, and a lack of documentation precludes any assessment of further potential for the released species.

Biocontrol by the introduction of exotic entomophages has been conducted against introduced pests and many entomologists may consider this as its only application. However, native pests are an equally suitable, yet neglected target for biocontrol (Carl 1982). In fact, a recent analysis of biocontrol introductions[1] shows that "new" parasitoid-host associations have been significantly more successful than "old", suggesting a considerable potential against native pests.

From an initial survey of the European literature (Mills 1983), we have identified seven spruce and fir tortricids as potential hosts of entomophages for trial against spruce budworm. Within the entomophage complexes of these hosts, predators are rarely dominant, but parasitoids could be important natural control factors maintaining host populations at endemic levels.

Since 1982, we have been investigating the biology and ecology of the parasitoids of European budmoths, on behalf of the Canadian Forestry Service, to select suitable candidates for trial against *C. fumiferana*. Earlier interest centered on two specific univoltine parasitoids, *Apanteles murinanae* and *Cephaloglypta murinanae*, of the closely related European fir budmoth *C. murinana* (e.g., Miller and Angus 1971). However, these parasitoids would be direct competitors of congeners dominant in the native complex. In addition, recent experimental studies of a perhaps synonymous parasitoid, *C. laricis* from Japan, indicate incompatibility with *C. fumiferana* due to encapsulation (Varty 1976).

Thus, candidate species must be carefully selected and prerelease compatibility trials are necessary in the biocontrol of native pests before releases can be attempted with any probability of success. We believe that candidate species from Europe should be univoltine to be independent of alternative hosts and therefore capable of responding to changes in host density; of broad geographic range to enhance climatic adaptability; and oligophagous in host range to increase the potential for adaptation to a new host and yet retain the ability to specialize on it. From our observations of parasitoids of European budmoths, we have found that ichneumonids of the genera *Diadegma* and *Enytus* show these characteristics and additionally, attack host larvae in the spring when there are no dominant native parasitoids.

Biocontrol by the introduction of natural enemies has been notably successful against many introduced forest pests in North America, providing long-term control with minimal environmental impact. The potential is there to develop similar control programs against native forest pests, such as that currently being undertaken for the eastern spruce budworm. However, we must avoid the uncertainty of earlier biocontrol programs through detailed prerelease research to maximize the probability of success and develop sound criteria for the use of exotic entomophages against native hosts.

Acknowledgment

This work was initiated and funded by the Canadian Forestry Service.

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[1] Hokkanen, H. 1983. Interspecific homeostasis, pest problems, and the principles of classical biological control. Unpublished Ph.D. Thesis, Cornell University.

Literature Cited

Campbell, R.W.; Beckwith, R.C.; Torgersen, T.R. 1983. Numerical behavior of some western spruce budworm (Lepidoptera:Tortricidae) populations in Washington and Idaho. Environ. Entomol. 12:1360-1366.

Carl, K.P. 1982. Biological control of native pests by introduced natural enemies. Biocontr. News & Inform. 3:191-200.

Clausen, C.P. 1978. Introduced parasites and predators or arthropod pests and weeds: a world review. U.S. Dep. Agric., Agr. Res. Serv., Washington, D.C. Agr. Handb. No. 480. 545 p.

McNamee, P.J.; McLeod, J.M.; Holling, C.S. 1981. The structure and behavior of defoliating insect/forest systems. Res. Popul. Ecol. 23:280-298.

Miller, C.A.; Angus, T.A. 1971. *Choristoneura fumiferana* (Clemens), spruce budworm (Lepidoptera: Tortricidae). Pages 127-130 *in* Comm. Inst. Biol. Contr., Techn. Commun. No. 4, Comm. Agr. Bur., Farnham Royal, England.

Mills, N.J. 1983. Possibilities for the biological control of *Choristoneura fumiferana* (Clemens) using natural enemies from Europe. Biocontr. News & Inform. 4:103-125.

Varty, I.W. 1976. Arthropod predators and parasitoids. Pages 103-105 *in* Proc. Symposium on the spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Misc. Publ. No. 1327.

Discussion Group B — Biorationals

Sex Pheromone Chemistry and Pheromone-Mediated Behavior of Spruce Budworm Moths

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We are examining the sex pheromone chemistry and pheromone-mediated behavior of three important coniferophagous budworms in the *Choristoneura* genus. Two eastern species, the spruce budworm (*Choristoneura fumiferana* (Clemens)), jack pine budworm (*Choristoneura pinus pinus* Freeman) and one western species, the western spruce budworm (*Choristoneura occidentalis* Freeman). These studies are in support of potential monitoring and control programs for these insects using pheromones. The major components of the female-produced sex pheromones are comprised of a group of congeneric mono-unsaturated C_{14} aldehydes, acetates and alcohols with blends, geometrical isomer ratios and release rates specific to each species (Table 1).

Sex Pheromone Chemistry and Behavior

We re-examined early work (Sanders and Weatherston 1976) on the sex pheromone chemistry of the spruce budworm and showed that female pheromone glands contained predominantly Δ11-14:Ac (20-40 ng/insect) (Wiesner et al. 1979); additionally we found Δ11-14:Ald (1-2 ng/insect) and Δ11-14:OH (1-2 ng/insect) all in a 95/5, *E/Z* ratio, and the saturated analogs of these components were also present at about 1 percent of the corresponding *E*-isomers (Silk et al. 1980). In contrast, we found (Silk et al. 1980, Table 1) that effluvia from calling females contained predominantly *E/Z*11-14:Ald (95/5, 10-40 ng/insect/night or about 1-5 ng/hour) along with 14:Ald at about 2 percent of the *E*-aldehyde), and traces of *E*11-14:Ac ($\leq$0.1 percent of *E*11-14:Ald); no alcohols were detected in female emissions. Preliminary field data showed no significant differences in trap capture between traps baited with a PVC rod containing all four components (in ratios similar to a calling female) compared to traps baited with the primary components, the *E/Z*-unsaturated aldehydes, alone. These tests (Silk et al., 1980) also verified that the addition of *E* 11-14:Ac to 95/5 *E/Z*11-14: Ald reduced trap captures. However, the effect of the acetate appeared to be negated by the presence of the saturated aldehyde but this occurred only when these additional components were present in female effluvia ratios.

The possibility that other chemical cues might be involved in close range behavior was not considered until recent work (Alford et al. 1983) in a laboratory wind-tunnel showed that a greater percentage of males initiated upwind flight and continued on to contact the source when about 5 percent 14:Ald was added to 95/5 *E/Z*-14:Ald. Similar results were obtained in the field (Alford et al. 1983). The addition of *E*11-14:Ac, at any level, to the primary components decreased the males' responsiveness to the aldehydes, but this affect appeared to be counteracted or altered by the presence of 14:Ald confirming our earlier trapping data (Silk et al. 1980). These findings were later confirmed in independent studies (Sanders 1984). In other field observations, unfractionated female volatile material, when added to the primary components, increased percentage contact significantly, again pointing to the existence of additional pheromone components.[1]

Similar work was carried out with the western spruce budworm (*C. occidentalis*) (Silk et al. 1982; Alford and Silk 1984) and the jack pine budworm (*C. pinus pinus*) (Silk et al. 1985; see Table 1). With *C. pinus pinus*, PVC rods (0.1 percent W/W) were as effective as virgin females in capturing males. Further behavioral work with this insect is being conducted; preliminary wind-tunnel analysis indicates that this blend is not equivalent to female-produced sex pheromone.

Field Tests

We have been involved in several major field tests: San Quentin, N.B. in 1978[2] and in Machias in 1980[3] in which we assessed the laboratory and field performance of the Conrel® (San Quentin) and the Hercon® (Machias) controlled-release formulations for spruce budworm pheromone (Wiesner and Silk 1982). The latter formulation proved very satisfactory in terms of its release characteristics in the field; similar experiments were conducted in Ontario in 1982 (Sanders and Silk 1982); a review of this work is presented elsewhere (Silk and Kuenen 1984).

Pheromone releaser distribution and/or point source release rates were found to have pronounced effects on the disruption of trap captures of the spruce budworm (Alford and Silk 1983). Small field plot studies with hand-placed Hercon® releasers in moderate to high density budworm populations indicated an increase in

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[1] Silk, P.J. 1983. New Brunswick Department of Natural Resources Report 1982-83. RPC Report #C/82/128; 6398. The assessment of the potential of the sex pheromone for controlling epidemic populations of spruce budworm. Unpublished.

[2] Dimond, J.B.; Mott, D.G.; Kemp, W.P.; Krall, J.H. 1984. A field test of mating-suppression using the spruce budworm sex pheromone. Tech. Bull. 113, Me. Agr. Exp. Stn., 21 pp.

[3] Miller, C.A. 1978. Report of spruce budworm pheromone trials, Maritimes. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. File Report 1980.

Table 1
Sex pheromones isolated and identified from budworm females

	*Pheromone components**		
Insect	*Primary*	*Secondary*	*Reference***
C. fumiferana	*95/5 **E/Z**11-14:Ald*	*14:Ald*	*Silk et al. 1980*
C. occidentalis	*92/8 **E/Z**11-14:Ald*	*89/11 **E/Z**11-14:Ac* *85/15 **E/Z**11-14:OH*	*Silk et al. 1982*
C. pinus pinus	*85/15 **E/Z**11-14:Ac (90%)* *85/15 **E/Z**11-14:OH (10%)*		*Silk et al 1985*

* *E/Z*11-14:Ald = *E/Z*11-tetradecenal; *E/Z*11-14AC = *E/Z*11-tetradecenyl acetate; *E/Z*11-14:OH = *E/Z*tetradecen-1-ol; 14:Ald = tetradecanal.

**A more complete list of contributors to *Choristoneura* sex pheromone chemistry can be found in Silk and Kuenen (1984).

trap disruption as the point sources of the synthetic pheromone were increased in release rate and decreased in number per unit area; an optimum in spacing and point source release rate was determined.

Literature Cited

Alford, A.R.; Silk, P.J. 1984. Behavioral effects of secondary components of the sex pheromone of the western spruce budworm (*Choristoneura occidentalis*) Free. J. Chem. Ecol. 10:265-270.

Alford, A.R.; Silk, P.J. 1983. Effect of pheromone releaser distribution and release rate on the mating success of the spruce budworm. J. Econ. Entomol. 76:774-778.

Alford, A.R.; Silk, P.J.; McClure, M.; Gibson, C.; Fitzpatrick, J. 1983. Behavioral effects of secondary components of the sex pheromone of the spruce budworm *Choristoneura fumiferana* Clem., Can. Entomol. 115:1053-1058.

Sanders, C.J.; Silk, P.J. 1982. Disruption of spruce budworm mating by means of Hercon plastic laminated flakes. Ontario 1981. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. Inf. Rep. O-X-335, 22 p.

Sanders, C.J.; Weatherston, W. 1976. Sex pheromone of the eastern spruce budworm (Lepidoptera:-Tortricidae) optimum blend of *trans*- and *cis*-11-tetradecenal. Can. Entomol. 108:1285-1290.

Sanders, C.J. 1984. Sex pheromone of the spruce budworm (Lepidoptera:Tortricidae): Evidence for a missing component. Can. Entomol. 16:83-100.

Silk, P.J.; Tan, S.H.; Wiesner, C.J.; Ross, R.J.; Lonergan, G.C. 1980. Sex pheromone chemistry of the eastern spruce budworm. Environ. Entomol. 9:640-644.

Silk, P.J.; Wiesner, C.J.; Tan, S.H.; Ross, R.J.; Grant, G.G. 1982. Sex pheromone chemistry of the western spruce budworm *Choristoneura occidentalis* Freeman, J. Chem. Ecol. 8:351-362.

Silk, P.J.; Kuenen, L.P.S.; Tan, S.H.; Roelofs, W.L.; Sanders, C.J.; Alford, A.R. 1985. Identification of sex pheromone components of the jack pine budworm, *Choristoneura pinus pinus* Freeman. J. Chem. Ecol. 11:159-167.

Silk, P.J.; Kuenen, L.P.S. 1984. Sex pheromones and their potential as control agents for forest Lepidoptera in eastern Canada. *In* W.Y. Garner and J. Harvey Jr. eds. Chemical and Biological Controls in Forestry. ACS Symposium Series 238. 406 p.

Wiesner, C.J.; Silk, P.J.; Tan, S.H. Palaniswamy, P.; Schmidt, J.O. 1979. Components of the sex pheromone gland of the eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera:Tortricidae). Can. Entomol. 11:1311.

Wiesner, C.J.; Silk, P.J. 1982. Monitoring the performance of eastern spruce budworm pheromone formulations. *In* B.A. Leonhardt and M. Beroza, eds. Insect Pheromone Technology: Chemistry and Applications. ACS Symposium Series 190. ACS Washington, D.C. 1982.

Discussion Group B —
Biorationals

Trichogramma vs. the Spruce Budworm

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Research on the use of *Trichogramma minutum* Riley as a biological control agent against the spruce budworm was initiated in cooperation with Daniel T. Jennings, USDA, Forest Service, Northeastern Forest Experiment Station at Orono, Maine. Research efforts encompassed laboratory studies on the basic biology and potential of this parasitoid plus field studies dealing with augmentative releases and alternate host abundance.

Laboratory studies dealt with mass rearing aspects such as parasitoid size and virulence, progeny production, longevity, and sex ratios, plus developmental rates and recycling of parasitoids following release in spruce budworm, and host-age acceptability by *T. minutum*.

Southard (et al. 1982) found that female *T. minutum* from spruce budworm (*Choristoneura fumiferana* (Clem.)) (large host) eggs were significantly larger for all body dimensions than *T. minutum* from *Sitotroga cerealella* (Olivier) (small host) eggs. A significant reduction in female parasitoid size was observed during the initial generations of *T. minutum* reared in the smaller host. However, this size reduction was not permanent. Following numerous generations in the *S. cerealella* host eggs, a significant increase in female parasitoid size was noted within the first generation of *T. minutum* reared in spruce budworm host eggs. Potential ramifications for manipulating *Trichogramma* size are substantial. A relatively inexpensive, easily-reared host, such as *S. cerealella* could be used for long-term colony maintenance. Then prior to field releases, rearing at least one generation in a larger host might provide greater fecundity and larger, more virulent parasitoids.

Mean daily progeny production by *T. minutum* ("Maine strain") was 15.2 in *C. fumiferana* and 10.9 in *S. cerealella* eggs (Houseweart et al. 1983). Laboratory results on progeny production, longevity, and sex ratios suggest a significant advantage for using spruce budworm eggs as hosts for rearing the "Maine strain" of *T. minutum*, especially for a higher female portion of progeny produced. However, parasitoids utilizing *S. cerealella* eggs lived longer. For inundative releases, increased longevity is probably not as advantageous as the early progeny production and the female-favored sex ratios. Regardless of these advantages, one must still consider rearing cost of the relatively cheap, easily-produced *S. cerealella* versus larger hosts. These laboratory results also point out another important factor to consider for augmentative releases: regardless of host used, progeny production drops off quickly following the first two days of oviposition, thus suggesting the merit of multiple, closely-timed releases versus single or widely-spaced releases.

Knowledge of the length of availability, the shape of the egg-deposition curve, and the age acceptability of spruce budworm eggs are important prerequisites for successful utilization of *T. minutum* in augmentative release programs. Houseweart et al. (1982) report that in both 1979 and 1980, budworm egg masses were deposited over a period of 27 days in the field. The egg deposition curve approximated a normal bell-shaped curve. Acceptability of spruce budworm eggs to *T. minutum* parasitism is dependent on the host's physiological age. Parasitism rates are greater during the younger stages of host egg development.

Development rates of *T. minutum*, were studied using three constant temperatures (14, 21, and 27°C) to provide information required in timing field releases of *T. minutum* for suppression of spruce budworm egg populations (Lawrence et al.). Development of *T. minutum* required the fewest degree days at 27°C, but longevity was greatest at 21°C. At all temperatures, *T. minutum* developed more rapidly in *S. cerealella* eggs than in *C. fumiferana* eggs. Calculations of day degree temperatures during the budworm egg deposition period showed that released *T. minutum* would develop fast enough to emerge and attack the last portion of the eggs deposited.

Spruce budworm egg masses were sampled in February and March to determine if budworm eggs harbor overwintering *T. minutum* as a potential stock source for mass rearing programs (Jennings and Houseweart 1983). Parasitized eggs contained only cadavers of *T. minutum* pupae; thus, there is no evidence that this species or any other egg parasitoid overwinters in eggs of the spruce budworm.

Field studies included both augmentative releases of *T. minutum* and a study of alternate hosts and characteristics of forest stands supporting native populations of *T. minutum*. Field releases of *T. minutum* for suppression of epidemic spruce budworm egg populations were conducted in Maine from 1977 to 1981 (Houseweart et al. 1984b). In 1977 and 1978, point-source releases using both commercial California and native Maine parasitoids indicated that the native Maine strain performed better. In 1979, broadcast and multiple releases showed slight improvement in parasitism over the four-point releases. In 1981, three closely-timed aerial, broadcast releases from a helicopter yielded significant increases in parasitism rates over control plots, but were not sufficient to suppress epidemic spruce budworm populations. Important variables were identified for future aerial releases.

Alternate hosts may influence levels of natural parasitism of spruce budworm eggs (Miller 1953, 1963; Neilson 1963). In 1979-80, Houseweart et al. (1984a) identified the key alternate hosts used by *Trichogramma* in Maine. One key overwintering host is the forest tent caterpillar. Alternate hosts available before budworm eggs are deposited may be used as natural reservoirs to increase *Trichogramma*. Additionally, alternate host parasitism levels might be used as indicators to allow adjustments of parasitoid numbers released for suppression. A new species of *Trichogramma* was discovered; *T.* sp. near *nubilale* (BIIL Culture No. *630-22-X-1*). This new species was recovered from both spruce budworm and forest tent caterpillar eggs.

Through regression techniques, identification of forest stands which supported high populations of *Trichogramma* indicated that stands with high basal area percentages of alder and larch and low basal areas of oak have the highest levels of parasitism. However, models must be verified with more field data before predictions may be made.

Literature Cited

Houseweart, M.W.; Southard, S.G.; Jennings, D.T. 1982. Availability and acceptability of spruce budworm eggs to parasitism by the egg parasitoid, *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). Can. Entomol. 114:657-666.

Houseweart, M.W.; Jennings, D.T.; Welty, C.; Southard, S.G. 1983. Progeny production by *Trichogramma minutum* (Hymenoptera:Trichogrammatidae) utilizing eggs of *Choristoneura fumiferana* (Lepidoptera: Tortricidae) and *Sitotroga cerealella* (Lepidoptera: Gelechiidae). Can. Entomol. 115:1245-1252.

Houseweart, M.W.; Jennings, D.T.; Pease, S.H.; Lawrence, R.K. 1984a. Alternate insect hosts and characteristics of forest stands supporting native populations of *Trichogramma minutum* Riley. CFRU Res. Bull. 5 (Maine Agric. Exp. Stn. Rep. No. 300). 32 p.

Houseweart, M.W.; Jennings, D.T.; Lawrence, R.K. 1984b. Field releases of *Trichogramma minutum* (Hymenoptera:Tortricidae) for suppression of epidemic spruce budworm, *Choristoneura fumiferana* (Lepidoptera:Tortricidae), egg populations in Maine. Can. Entomol. 116:1357-1366.

Jennings, D.T.; Houseweart, M.W. 1983. Parasitism of spruce budworm (Lepidoptera:Tortricidae) eggs by *Trichogramma minutum* and absence of overwintering parasitoids. Environ. Entomol. 12:535-540.

Lawrence, R.K.; Houseweart, M.W.; Jennings, D.T.; Halteman, W.A. 1985. Development rates of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) and implications for timing augmentative releases for suppression of egg populations of *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 117:556-563.

Southard, S.G.; Houseweart, M.W.; Jennings, D.T.; Halteman, W.A. 1982. Size differences of laboratory reared and wild populations of *Trichogramma minutum* (Hymenoptera:Trichogrammatidae). Can. Entomol. 114:693-698.

Miller, C.A. 1953. Parasitism of spruce budworm eggs by *Trichogramma minutum*. Can. Dep. Agric., Sci. Serv., Div. of For. Biol., Bi-mon. Prog. Rep. 9:1.

Miller, C.A. 1963. Parasites of the spruce budworm. Pages 228-244 *in* R.F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332 p.

Neilson, M.M. 1963. The analysis of egg survival in the unsprayed area. Pages 37-41 *in* R.F. Morris, ed., The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. 31. 332 p.

Discussion Group B —
Biorationals

Disruption of Spruce Budworm Mating by Sex Pheromone

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Attempts to disrupt the mating of spruce budworm by aerial application of pheromone in Ontario with microcapsules in 1975, Conrel® fibres in 1977 and Hercon® flakes in 1981 caused large reductions in the numbers of male moths caught in traps, but evidence for reduction of mating and of numbers of fertile eggs has been inconclusive. Invasion by fertile females has always been a possibility and in the most recent trial, 1981, it appears that the sticker was too dilute and the Hercon® flakes did not adhere to the foliage. Arrangements are being made to equip the Canadian Forestry Service's Cessna 188 with dispensing equipment to test stickers in Ontario.

Wind tunnel experiments showed that a formulation in which each particle emits pheromone at a higher rate than a female moth is more effective for disruption than one in which the same amount of pheromone is released from numerous less potent particles (Sanders 1982). Presumably the more potent lures out-compete the females. If true the synthetic pheromone must be as attractive as possible, and considerable effort has gone into ensuring this.

Recent tests showed that the known components of the pheromone, including (E)-11-tetradecenyl acetate and tetradecanal at the same concentrations as in the female-emitted pheromone (Silk et al. 1980), are not as effective as the natural pheromone (Sanders 1984).

Further tests have been carried out with a wide range of concentrations of tetradecanal. No significant improvement in attraction was recorded (Figure 1). When attracted to rubber septa loaded with 100 µg TDAL, 31 percent of the males made copulatory attempts on the septum. Additions of 1, 10, and 100 µg tetradecanal raised this to 41, 55, and 49 percent respectively: significant improvements but still well short of the 100 percent response evoked by females.

The search for the missing component is continuing because of the importance of using a formulation which can outcompete calling females, and it is recommended that further field trials of mating disruption should await not only an adequate sticker for the formulations but also for the identification of a more potent pheromone blend.

Literature Cited

Sanders, C.J. 1982. Disruption of male spruce budworm orientation to calling females in a wind tunnel by synthetic pheromone. J. Chem. Ecol. 8:493-506.

Sanders, C.J. 1984. Sex pheromone of the spruce budworm (Lepidoptera:Tortricidae): Evidence of a missing component. Can. Entomol. 116:93-100.

Silk, P.J.; Tan, S.H.; Wiesner, C.J.; Ross, R.J.; Lonergan, G.C. 1980. Sex pheromone chemistry of the eastern spruce budworm, *Choristoneura fumiferana*. Environ. Entomol. 9:640-644.

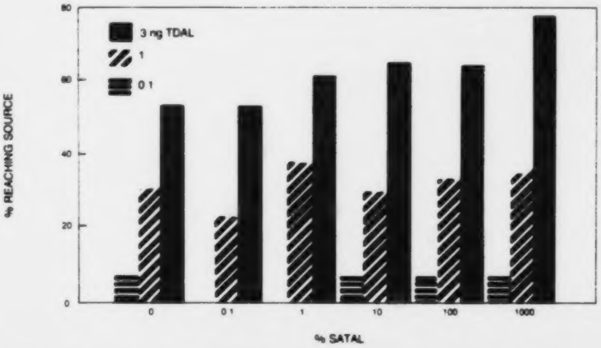

Figure 1. Percentages of male spruce budworm attracted in a wind tunnel to various blends and concentrations of 95:5 (E:Z)-11-tetradecenal (TDAL) and the saturated aldehyde, tetradecanal (SATAL), applied to filter paper.

Discussion Group B —
Biorationals

Feasibility Testing of Inundative Releases of the Parasitoid, *Trichogramma minutum*, against Spruce Budworm in Ontario

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Inundative releases of parasites, especially *Trichogramma* spp. are used to suppress agricultural insect populations in the United States, China, and the U.S.S.R. Field tests to investigate the potential of this tactic against spruce budworm in Maine received brief support from CANUSA in the early 1980s.

In 1981, the Ontario Ministry of Natural Resources (OMNR) initiated a cooperative research program, involving OMNR, University of Guelph, University of Toronto, and the Great Lakes Forest Research Centre (GLFRC) (Canadian Forestry Service). The objectives of the program were:

1. To develop the technical capability to mass produce *Trichogramma minutum* (T.m.), a native parasite of spruce budworm, (*Choristoneura fumiferana* (Clem.)), at the University of Guelph.
2. To determine the effect of various schedules and levels of inundative release of T.m. on parasitism of spruce budworm eggs. This phase was carried out by the University of Toronto, using ground releases. The effects of different environmental and rearing conditions were also investigated.
3. To develop methods of aerial release of T.m. This phase was carried out by OMNR.

Staff from GLFRC assisted in assessing the parasitism levels of budworm eggs in the field.

Research Program

Mass Production OMNR is providing financial support for a 3.5-year project at the University of Guelph to develop the technology to mass rear T.m. The initial attempt in 1981/82, which involved the use of *Anagasta kuehniella* as the host for T.m., was generally unsatisfactory. In 1983, the University of Guelph improved the rearing facility and changed to *Sitotroga cereallela* as the host. The result has been a dramatic increase in production capability. With this technology, the existing facility is producing 120 million T.m. per month, but could produce over 300 million per month.

Ground Releases In 1982 and 1983, T.m. were released on the ground in a 20-year-old white spruce/balsam fir stand near Hearst in northern Ontario. Populations of spruce budworm were high (>200 egg masses/9.29 m^2 [100 ft^2]) but natural T.m. parasitism was low (<4 percent of egg masses). Parasitism was monitored using a continuous supply of fresh, lab-reared budworm egg masses (sentinel egg masses) distributed randomly throughout the stand. In ground release trails, host eggs containing T.m. pupae were dispersed on a 7-m (23-ft) grid throughout the plots, 25 cm (10 in.) above ground level. In 1982, the supply of T.m. was very low because of production difficulties, and the release density on the plots (0.25 ha.) was only 480,000 female T.m./ha (195,000/acre), resulting in an average parasitism level of 16 percent. Release rates in 1983 were increased, and on plots receiving 12 million female T.m./ha (4.8 million/acre), parasitism of sentinel budworm egg masses averaged 87 percent. At this release rate, 80 percent of the eggs within each egg mass were parasitized.

Parasitism of *natural* spruce budworm egg masses is dependent upon the proportion of fresh egg masses (<4 days old) present at the time of parasite release. Assessment of the ground releases indicated that the 1983 releases resulted in large increases in parasitism of natural egg masses. On white spruce, 41 percent of the egg masses checked were parasitized, and on balsam fir, 64 percent were parasitized. In about 60 percent of the egg masses, over 75 percent of the eggs were parasitized. In untreated plots, parasitism was less than 1 percent.

Aerial Releases OMNR has developed an aerial dispersal mechanism for use on a helicopter, which will deliver T.m. parasitized eggs at specific rates. Aerial releases were carried out in 1982 and 1983 in the same general area as the ground releases. Insufficient T.m. were produced in 1982 to permit a meaningful test of parasitism; T.m. were released at 250,000 females/ha (101,000/acre), which was insufficient to affect parasitism levels. However, valuable experience was gained about handling, shipping, calibration, and dispersal of

T.m. In 1983, one aerial release was carried out, timed for the middle of the budworm oviposition period. T.m. were released at the rate of 6.5 million females/ha (2.6 million per acre) in a 2-ha (5-acre) plot. Parasitism rates of 22 percent on spruce and 28 percent on fir were observed in the release area, compared with less than 1 percent in untreated areas. Furthermore, in 55 percent of the egg masses, over 75 percent of the eggs were parasitized.

Summary To date, the program has shown that inundative releases can achieve high levels of parasitism (>50 percent) in spruce budworm eggs. As well, the technology is available to aerially disperse T.m. in forest stands. The technology to mass produce T.m. has been developed to the point where large scale production is possible in Canada. The unit cost will be highly dependent upon production levels.

Discussion Group B —
Biorationals

Development of *Bacillus thuringiensis* for Control of Spruce Budworm: Recent Work in Maine

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In 1979, Thuricide® 16B formulation of *Bacillus thuringiensis* (B.t.) was applied to five, 40-ha (100-acre) plots of spruce-fir forest type at rates of 20 BIU per ha (8 BIU/acre), using Bell 47 helicopters. Additional treatments compared with this standard were the same quantity of B.t. plus chitinase (82 mg/ha, 33 mg/acre) and the same quantity of B.t. plus the chemical insecticide, acephate (56 gms/ha, 23 mg/acre). All treatments provided satisfactory protection of balsam fir and red spruce foliage in spite of prespray budworm numbers of 45-70 per 45-cm branch. There was some indication that B.t. plus acephate produced slightly better control, however, differences were not statistically significant. No beneficial effect of chitinase was demonstrated (Dimond and Spies 1980).

In similar tests in 1980, comparisons were made between several B.t. products (Dimond et al. 1981). Dosage rates were all 20 BIU/ha (8 BIU/acre), but spray emission rates varied. Thuricide® 16B was applied at 9.3 L/ha (1 gal/acre), Thuricide® 24B at 4.7 L/ha (0.5 gal/acre), and Dipel® 4L was applied at three rates, 9.3, 4.7, and 2.4 L/ha (1 gal, 0.5 gal, and 0.25 gal/acre). The latter was an application of undiluted, or "neat," Dipel®. Small plots were replicated five times for each treatment, and applications were made with small, fixed-wing aircraft with standard boom and nozzle.

No treatments produced statistically significant population reductions, but most showed significant levels of foliage protection. Lower than anticipated efficacy was a result of prolonged wet weather. There were no significant differences between formulations, or between spray emission rates of 9.3 and 4.7 L/ha (1 gal and 0.5 gal/acre). The treatment of neat Dipel® produced very poor spray deposit on agar plates and marginal efficacy.

Tests in 1982 were a portion of the CANUSA B.t. cooperative field test (Lewis et al., 1984). A single formulation, Thuricide® 32 LV, was tested at dosage rates of 20, 30, and 40 BIU/ha (8, 12, and 16 BIU/acre) and at spray emission rates of 9.3 and 4.7 L/ha (1 gal and 0.5 gal/acre). Applications involved the same aircraft as in 1980, and plots were small and replicated five times.

We found, in Maine, that 30 BIU (12 BIU) was superior to 20 BIU (8 BIU), but that 40 BIU (16 BIU) gave little further advantage. There was no difference between the two dilution rates. Weather was favorable, and results with the higher dosages were satisfactory.

In a separate test in 1982, Dipel® 4L and Dipel® 6L were each applied in undiluted form to single, 162-ha (400-acre) blocks of forest. Spray emission rates were 2.4 and 1.8 L/ha (0.25 and 0.19 gal/acre), respectively, and Micronair® nozzles were used. Agar plates showed excellent spray deposit, and results of both treatments were highly satisfactory in terms of population reduction and foliate protection, and on both fir and red spruce (Dimond 1982).

The 1983 tests involved a comparison of the new NRD-12 strain of B.t., formulated as Thuricide® 32LV, with commercial Thuricide® 32LV. Spray blocks were single blocks of 120-200 ha (300-495 acres). Dosage was 30 BIU/ha (12 BIU/acre) at a spray emission rate of

4.7 L/ha (0.5 gal/acre). Results supported laboratory assays (N. Dubois, personal communication) that suggest NRD-12 is more effective than the commercial strain of B.t. This work is not yet published.

Additional work in Maine involved a cooperative study of susceptibility of the different larval instars of the budworm to B.t. (Fast and Dimond 1984). Both laboratory and small field tests suggest that instars 4, 5, and early 6 are equally susceptible to B.t.; Instar 3 may be somewhat more difficult to kill (Madore 1982). The "spray window" for B.t. is not necessarily more narrow than with chemical insecticides.

Literature Cited

Dimond, J.B. 1982. Effects of aerial sprays of undiluted *Bacillus thuringiensis* formulations on spruce budworms. Maine Agricultural Experiment Station, University of Maine, Orono, ME. Misc. Rep. No. 274. 9 p.

Dimond, J.B.; Spies, C.J. 1980. A comparison of B.t. alone with B.t. plus chitinase and Orthene in control of eastern spruce budworm. Maine Agricultural Experiment Station, University of Maine, Orono, ME. Misc. Rep. No. 274. 15 p.

Dimond, J.B.; Spies, C.J.; O'Neal, J. 1981. Spruce budworm: evaluations of B.t. trials in Maine, 1980. Maine Agricultural Experiment Station, University of Maine, Orono, ME. Misc. Rep. No. 237. 15 p.

Fast, P.G.; Dimond, J.B. 1984. Susceptibility of larval instars of spruce budworm, *Choristoneura fumiferana* (Lepidoptera:Tortricidae), to *Bacillus thuringiensis*. Can. Entomol. 116: 131-137.

Lewis, F.B.; Walton, G.S.; Dimond, J.B.; Morris, O.N.; Parker, B.; Reardon, R.C. 1984. Aerial application of B.t. against spruce budworm. 1982 CANUSA B.t. cooperative field tests-combined summary. J. Econ. Entomol. 77:999-1003.

Madore, C.D. 1982. Bioassays with *Bacillus thuringiensis* Berliner var. *Kurstaki* against spruce budworm, *Choristoneura fumiferana* (Clem.): inter-instar susceptibility. M.S. Thesis, University of Maine, Orono, ME, 30 p.

Discussion Group B —
Biorationals

Summary

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In the discussion about the use of pheromones for suppression of spruce budworm populations, it was apparent that, in spite of ample evidence of male confusion based on catches in baited traps, there have been no indications of population reductions in the field. The view in the East is that field studies should be suspended until more is known. Recent studies in the East suggest that reacting males are orienting to point sources of pheromone. The exact and most attractive blend of pheromone chemicals must still be identified, to make artificial point sources of pheromone competitive with actual females. The optimum dispersion of artificial point sources must also be identified. The belief in the West is that the optimal pheromone blend for *C. occidentalis* has been identified. Future field tests will concentrate on low populations where the practical benefits of pheromone applications are more likely to occur.

The discussions of *Bacillus thuringiensis* (B.t.) revealed substantial progress in the practical application of the control procedure in recent years. Substantial operational use of B.t. now occurs in several jurisdictions, with greater use anticipated. This mode of development, based on new, concentrated formulations, may be reaching an endpoint. New breakthroughs may come from selection of more potent strains or through genetic engineering of the B.t. organism.

Technology of mass release of *Trichogramma* egg parasites showed considerable advancement, particularly in the studies reported from Ontario. The important consideration now is the economics of use of the tactic in suppression programs. Where might this fit into a practical IPM program?

The papers on the introduction of exotic parasitoids of the budworm, and on exploitation of modified viruses from hosts other than the budworm, suggest interesting approaches, although these are in their early stages now. We look forward to attempts to further develop and apply the concepts.

Discussion Group C —
Applications Technology

Deposit of Pesticide Sprays on Coniferous Foliage — A Summary of Work

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The first attempt to use aircraft for spraying spruce budworm occurred in Canada during 1944 (Nagel and Yuill 1947). Immediately researchers identified application problems which are nearly identical to problems facing today's applicator. As Craighead and Brown (1946) reported, "It is essential to obtain a more uniform coverage and less loss in the spray materials liberated from airplanes in order to economize on materials and to avoid injury to wildlife. The relation between the viscosity and density of the spray fluids, particle size, pattern of dispersal, height of flying, and the amount of DDT deposited on the foliage should be determined." Progress toward addressing these problems and improving aerial application was not apparent in the literature until Himel and Moore (1967) reported a relationship between pesticide drop size and mortality of western spruce budworm.

The USDA Forest Service (Forest Pest Management and Missoula Equipment Development Center) expanded on the Himel and Moore work with the objective to determine the size and number of pesticide drops which deposit on foliage. Defoliators are in direct contact with foliage — it is their food and their temporary shelter. If there were a range of drop sizes which deposit on foliage, would it not be useful to identify this range? Why disperse pesticides in drop sizes which are not observed and presumably do not deposit on foliage in significant number?

In pursuit of these questions, we examined coniferous foliage for presence of pesticide drops from seven aerial spray projects conducted by the USDA Forest Service from 1971 to 1981. Results were surprisingly consistent from project to project, even though formulations and application methods differed among projects. Results of our observations are summarized as follows:

1. The majority of pesticide drops observed on coniferous foliage were less than 60 microns in diameter, (Barry et al. 1977; Barry and Ekblad 1978; and Barry 1984).
2. Number of pesticide drops observed on coniferous needles collected from the lower crown by tree species were as follows:

Species	*Foliage density*	*Tank mix application per acre*	*Drops/cm of needle length*	*References*
Ponderosa pine	*open*	*1 GPA*	*1.05*	*unpublished*[1]
Douglas-fir	*dense*	*1 GPA*	*0.40*	*Barry (1984)*
Slash pine	*open*	*5 GPA*	*7.05*	*Barry et al. (1981)*
Ocala sand pine	*dense*	*5 GPA*	*0.75*	*Barry et al. (1981)*

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[1] Data from USDA Forest Service, Southwestern Region, pandora moth control project, Jacob Lake, AZ, 1981.

3. Number of pesticide drops impacting on coniferous foliage is related to several factors:
    a. Foliage density. Densely foliated trees, such as Ocala sand pine, collect fewer drops per needle than sparsely foliated species such as ponderosa pine and slash pine (Barry et al. 1984).
    b. Location on tree. A larger number of drops are observed in the upper crown compared to the lower crown (Barry et al. 1984).
    c. Spray volume. As expected, higher spray volumes, i.e. 5 GPA vs 1 GPA, result in more drops on foliage than lower spray volume.
    d. Application. Results (Barry et al. 1981) suggest that foliage in the upper crown, which intercepts the spray aircraft's wake, captures more drops than foliage outside the wake.
4. Most drops which penetrate the canopy and deposit on the forest floor are less than 100 microns in diameter. The larger drops are observed on samplers from open areas where the drops have not been screened by foliage (Barry et al. 1982).

In part we have answered the 1946 Craighead and Brown drop size question. What has not been answered is how to apply this knowledge and how it relates to the amount of active ingredient required on the foliage to provide effective control. This is a multidisciplinary challenge to our resourcefulness in conducting highly controlled field experiments on individual trees, branches, and needles. Until these questions are answered it will continue to be a hit and miss game.

Literature Cited

Barry, J.W.; Ciesla, W.M.; Tysowski, M.; Ekblad, R.B. 1977. Impaction of insecticide particles on western spruce budworm larvae and Douglas-fir needles. J. Ecom. Entomol. 70: No. 3, 387-388.

Barry, J.; Ekblad, R. 1978. Deposition of insecticide drops on coniferous foliage. Trans. ASAE 21: 438-441.

Barry, J.; Wong, J.; Kenney, P.; Barber, L.; Flake, H.; Ekblad, R. 1981. Deposition of pesticide drops on pine foliage from aerial application. Zeitschrift fur angewandte Entomologie, Sonderdruck aus Bd. 92, H.3, S. 224-232.

Barry, J.W.; Kenney, P.A.; Barber, L.; Ekblad, R.B.; Dumbauld, R.J.; Rafferty, J.E.; Flake, H.W.; Overgaard, N.A. 1982. Aerial application to southern pine seed orchards, data report of the Withlacoochee trials. U.S. Dep. Agric., Forest Service, Forest Pest Management, Asheville Field Office, Asheville, NC.

Barry, J.W.; Barber, L; Kenney, P.A.; Overgaard, N.A. 1984. Feasibility of aerial spraying of southern pine seed orchards. Southern Journal of Applied Forestry. 8(3) 127-131.

Barry, J.W. 1984. Deposition of chemical and biological agents in conifers Pages 117-137 *in* ACS Symposium Series 238, American Chemical Society, Washington, D.C.

Craighead, F.C.; Brown, R.C. 1946. Summary of 1945 DDT investigations for control of forest insects with special reference to aerial application, E684. U.S. Dep. Agric., Agricultural Research Administration, Bureau of Entomology and Plant Quarantine, Division of Forest Insect Investigations, Beltsville, MD.

Himel, C.M.; Moore, A.D. 1967. Spruce budworm mortality as a function of aerial spray droplet size. Science 156:1250-1.

Nagel, R.H.; Yuill, J.S. 1947. Field experiments with aerial sprays. U.S. Dep. Agric., Agricultural Research Administration, Bureau of Entomology and Plant Quarantine, Forest Insect Laboratory, Beltsville, MD.

Discussion Group C — Applications Technology

Field Studies by the National Research Council Canada on Wind Drift of Insecticide Sprays in New Brunswick

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Since 1982, the Unsteady Aerodynamics Laboratory of the National Research Council of Canada has been conducting field studies in New Brunswick (Crabbe et al. 1983, 1984) in conjunction with Forest Protection Limited (FPL), the New Brunswick Research and Productivity Council, the University of New Brunswick and the Atmospheric Environment Service of Environment Canada to determine the meteorological conditions that maximize forest canopy deposit (ULV) aerial forest insecticide sprays. The application strength of ULV sprays in typically under 0.5 kg of chemical active ingredient (AI) per hectare (0.5 lb AI/acre) and the maximum droplet diameter is generally under 300 microns so that most of the spray droplets have low sedimentary deposition. Consequently, the thermal stability and turbulence structure of the atmospheric surface layer have large influences on the off-target loss of such sprays to windborne drift.

In New Brunswick, FPL uses Grumman TBM spray planes equipped with Teejet® nozzles to atomize, in most cases, an aqueous fenitrothion formulation used against the spruce budworm. The application strength is 210 g AI (3 oz AI) in 1.5 kg/ha (0.6 lb/acre) with water 83 percent of the spray mass. Computations reveal that evaporation of even the largest droplet, ca 200 microns dia. (Tomney et al. 1978), is usually complete before the vortex wake, which contains the spray emission, reaches the tree tops from the flying altitude about 45 m (148 ft) above ground level (agl). In thermally stable conditions, the resulting droplets, which range from about 2 to 100 microns dia., will settle only slowly onto the canopy following vortex rebound and dissipation, giving rise to significant off-target loss of spray droplets to windborne drift. On the other hand, the effect of atmospheric turbulence, associated with thermally neutral to unstable conditions, is to transport ULV droplets downward onto the canopy at about the same rate as it transports fluid momentum downward onto the canopy under these conditions to balance the relatively high shearing stress between the wind and the trees.

Results from the 1983 ULV TBM spray trails in New Brunswick are tabulated below in terms of percent wind drift vs the (measured) turbulent transfer velocity, v_d at 24m (78.7 ft) agl.

These data show that one should avoid ULV aerial forest sprays in early morning stable conditions (Trial No. 5). Surprisingly, turbulent windy conditions (Trial No. 4) produce the lowest windborne loss of droplets to long-range drift, essentially because of the large value of the turbulent transfer velocity under these conditions. In near-neutral flow v_d, which is of the order of $-\overline{uw}/U$, where U is mean wind speed and u and w are longitudinal and vertical fluctuating wind velocity components, is invariant with wind speed so that the (Trial No. 4) results should continue to hold in higher wind speeds. In the 1984 field trials, the Unsteady Aerodynamics Laboratory plans to examine this hypothesis which, if proven valid, will greatly enlarge the daily spray window at minimal risk to bystanders.

Literature Cited

Crabbe, R.S.; Elias, L.; Davie, S. 1983. Field study of the effect of atmospheric stability on target deposition and effective swath widths for aerial forest sprays in New Brunswick. Part II. National Research Council of Canada, Ottawa, Ont. Report LTR-VR-65.

Crabbe, R.S.; McCooeye, M.; Elias, L. 1984. Effect of atmospheric stability on wind drift in aerial forest spray trials. Neutral to stable conditions. National Research Council of Canada, Ottawa, Ont. Report LTR-VA-65.

Tomney, T.D.; Smedley, J.B.; Kristmanson, D.D.; Picot, J.J.C. 1978. The characteristics of drop size distributions generated by aerial spray atomizers. Univ. of New Brunswick, Fredericton. Dep. of Chemical Engineering Report.

Windborne Spray Drift

Trial	*Time*	*Classification*	$v_d(24)$ *(cm/s)*	*Percent drift* 200m	400m	1200m	*U(46) (m/s/Deg M)*
1	*0825*	*slightly unstable*	*7*		*42*	*~3*	*2.9/275*
2	*0712*	*slightly stable*	*2*		*17*	*5*	*3.9/255*
3	*2023*	*slightly stable*	*3*	*15*	*7*	*3*	*5.2/235*
4	*0619*	*neutral*	*8*	*7*	*5*	*~2*	*5.5/191*
5	*0635*	*very stable*	*~0*	*55*	*50*	*17*	*3.3/258*

Discussion Group C — Applications Technology

Research Activities in the Pesticide Formulations Project at FPMI

A. Sundaram

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For effective control of forest pest insects and weeds, a pesticide should be formulated in an appropriate medium: to give good stability; to enable easy mixing, pumping, and storing capabilities under field conditions; to cause efficient atomization by the available spray equipment to result in target-specific droplet sizes; to provide droplets with good impaction and retention characteristics; to possess foliar stability just long enough for pest control during the critical period of insect development; and then to decompose rapidly into innocuous products.

Research studies undertaken in the Pesticide Formulations Project at the Forest Pest Management Institute can be grouped under three categories: herbicides, biorationals, and chemical insecticides.

Studies with herbicide formulations involve understanding the role of adjuvants on spray droplet spectra and on droplet impaction, retention, spreading, adhesion, and penetration characteristics. Contact angle measurements for the droplet-target interface are being carried out and the various physical forces and energies involved are being measured. Some of the studies completed recently are 1) spray adjuvants for drift control of herbicide droplets, 2) droplet impaction, retention and dissipation characteristics of four glyphosate formulations on nontarget conifer needles.

Studies with biorationals mainly involve investigations on spray droplet encapsulation, impaction, retention, and adhesion characteristics of various commercial formulations of *Bacillus thuringiensis* (B.t.). The influence of Triton B-1956 and tall oil as stickers of droplets on conifers is also being studied at different humidity and temperature conditions. Some of the studies completed recently are 1) droplet impaction characteristics of three B.t. formulations on new and mature conifer needles, 2) rainfastness of spray droplets of a B.t. formulation on conifer needles with and without the Rhoplex sticker.

Research with chemical insecticides involves two types of formulations: the basic formulation which is usually a commercial formulation as supplied by the manufacturer, and the tank mix formulation which is the commercial formulation plus the spray vehicle added by the end user and applicator.

Research carried out in the Pesticide Formulations Project with the basic formulation involves:

1. Storage stability of Active Ingredients (AI) under a range of temperatures including those during the winter months,
2. Rate of sedimentation and/or crystallization of AI and inerts over a 1-year period under a range of temperatures including those during the winter months,
3. Resuspensibility of sediments upon moderate agitation after storage over the winter,
4. Variations in mass of AI and mass of inerts for different lot numbers for quality control,
5. Variations in physical properties for different lot numbers for quality control,
6. Investigations to determine the optimum field diluent to be used in spray operations,
7. Investigations to determine the need for spray adjuvants for enhancing spray effectiveness and efficiency.

Studies that were recently completed involve three basic formulations, one from each of Chemagro (Matacil® 180F), Sumitomo Chemicals (Sumithion® 20%F), and Union Carbide (Zectran® UCZF19).

Research with the tank mix formulations covers a series of studies.

1. Stability studies involve investigations of phase separation of AI and inerts at a range of temperatures, with water of variable pH and hardness, and with spray adjuvants.
2. Relative atomization characteristic studies look at the effect of liquid properties on disintegration of ligaments and effect of additives, suspended particles, wetting agents and polymeric components on disintegration of ligaments.
3. Relative evaporation characteristic studies involve comparative evaporation of droplets and liquid films, evaporation of volatile components of formulations from biological surfaces.
4. Droplet retention and adhesion characteristic studies are related to the behavior of droplets on biological surfaces. Several formulations are being studied with and without adjuvants.
5. Studies on the influence of formulation component concentrations on droplet retention characteristics on buds, needles and stems of spruce and balsam fir have demonstrated the variability in the droplet absorption properties of different biological surfaces. Conifer needles absorb dilute formulations much more readily than the bud caps and bark surfaces.

In summary, research activities undertaken in the Pesticide Formulations Project have provided valuable information on formulation properties that are necessary for enhancing field performance of pesticide formulations under different application conditions.

Discussion Group C —
Applications Technology

Aerial Spray Navigation: Maine Spruce Budworm Suppression Project

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There are many possible areas for an error to occur during an aerial application of pesticides. You may have a wide variety of topography causing inconsistent spray release height and thereby affecting an alteration of swath width and application rate. Or you may have increases or decreases of application speed which could have a similar effect. But none of these (except gross error) can effect performance like poor line placement or inaccurate offset spacing.

There are two methods presently acceptable to the Maine Forest Service for navigation, or aircraft alignment. Visual navigation (reliance on visual check points and maps) and navigation by electronic guidance. In both cases there are limits to the accuracy that can be achieved in evaluating aircraft performance (line placement). It is still necessary to rely on the (USGS) topographic quadrangle maps, which do not exceed an accuracy of 1/30th of map scale.

For visual navigation, besides the inherent inaccuracies in the scale of the maps used, we must also be aware of the potential for additional error. The flight line must be drawn on maps indicating proper alignment of aircraft. On a map with nominal scale of 1:62,500, a simple pencil line (approximately 1/60 of an inch) would cover about 30 percent of a 300-foot (91-m) swath that could be translated into a potential 100- to 200-foot (30.5- to 81-m) placement error. Another consideration is the half swath required at the beginning of each spray block (Figure 1).

The difficulty of interpreting this half-width is implicit in the small spaces between adjacent flight line centers (See Table 1).

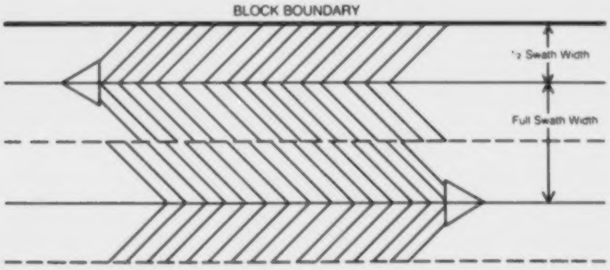


Figure 1. Diagram showing proper Half-swath offset.

Table 1
Swath width and corresponding grid space

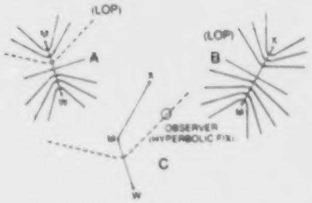
Swath width (Ft.)	*½ Grid space (In.)*
300	*0.058*
900	*0.173*
120	*0.230*

Estimating the center of such small spacing is difficult. Yet an error of only 25 percent could result in an omission or commission of over 36 acres per mile (9 ha/km) for a 1200-foot (366-m) swath.

Therefore, due to the high potential for error, visual navigation (although still acceptable) is only used in very special cases such as stripping and contour flying.

Electronic navigational systems have been used in Maine for a number of years. Most recently the system of choice has been the Loran-C.

Loran is a pulsed hyperbolic navigation system, that uses synchronized signals from three or more Loran transmitting stations to obtain a position fix. Essentially a Loran receiver measures the difference in arrival time of signals emitted from a master and two or more secondaries, these time differences create lines of position (LOP). When two LOP's are superimposed, as in Figure 2, the receiver position is known to be at their intersection.



The Loran system is very reliable. When a base line (first spray line or block boundaries) has been established, the Loran system can guide an aircraft accurately on that line or on any line parallel to the base line to within 50 feet (15 m).

In addition to linear guidance, the Loran receiver continually displays the longitude and latitude of the present position. By monitoring this continually updating display, an aircraft pilot can determine the location of lines perpendicular to the base line, such as block boundaries.

When compared with visual guidance, Loran proves to be superior and the system of choice by the Maine Forest Service.

Discussion Group C —
Applications Technology

Aerial Navigation of Spruce Budworm Spraying in New Brunswick

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New Brunswick spruce budworm spray programs have historically relied upon visual methods of spray aircraft navigation. During the 1950s Stearman biplanes operated in pairs in assigned blocks of about 1000 ha (2,471 acres) as far as possible defined by readily-identifiable topographical features. The lead pilot of each team was responsible for obtaining effective coverage with the correct gallonage of insecticide through previously-gained familiarity with the block, part-time observation by chief pilots, and professional skill.

The present system of aerial flagging was developed in 1961 for guidance of the larger, faster and less maneuverable TBM Avengers then replacing the Stearman as the New Brunswick workhorse (Flieger 1964). The present practice has been adapted over the years to meet evolving needs, as follows.

Areas to be sprayed are blocked out on 1:50,000 topographic maps. Parallel lines are plotted to indicate swaths to be covered by spray teams. The most common swath employed by Forest Protection Limited requires 134-m (440-ft) spacing between TBM's operating in two or three-plane teams, chiefly the latter. The aircraft line up at the required spacing in 45° echelon and fly at 150 knots.

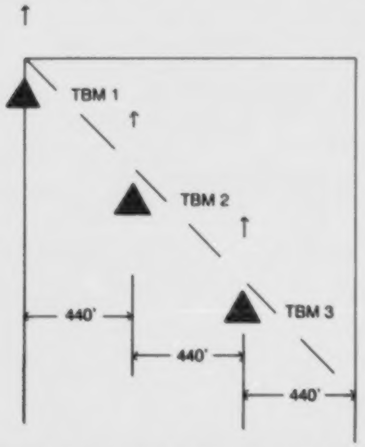

Figure 1. TBM spacing and alignment are shown for a right echelon formation.

"Aerial flags" are light aircraft of the Cessna 172 class each carrying a pilot and a "pointer" trained in low-level visual navigation. Pointer aircraft work in pairs, one designated as "lead pointer," the second as "number 2 pointer." Each pointer is equipped with the 1:50,000 maps prepared as above and records the following in-flight information:

1. Time of start and finish of spraying.
2. Wind direction and velocity (observational).
3. Temperature at start and finish.
4. Sky: clear, broken, overcast.
5. Spray action: settling, breaking, rising.
6. Deviations from plotted tracks, etc.

Pointer teams are responsible to "chief pointers" located at each operational base. The chief pointer is responsible for decisions concerning suitability of conditions for spraying in the blocks designated as ready for treatment by the project entomologist. Chief pointers also monitor spray and pointer teams in action and audit pointer reports. These are completed immediately following spraying and in addition to the above information, record complete block identification, insecticide, formulation, dosage and application rate, miles sprayed per load, haul distance, and spray team identity. Completed reports are signed by both pointers and the chief pointer.

Guidance is provided as follows. The lead pointer first establishes an orbit over the end of the first swath line ("initial point" or IP) and downwind of subsequent lines to avoid flying through drifting spray in subsequent "passes." No. 2 pointer establishes an orbit two or three miles behind, lining up on the spray line ahead. The spray team lines up in turn on the two pointers and commences an approach to the spray block. Upon a radio signal from the spray leader when about a mile from No. 2 pointer, the slower-flying pointers commence flying along the intended track at about 700 feet. No. 2 pointer endeavors to arrive above the IP at the same time as the spray leader in order to radio "booms on"

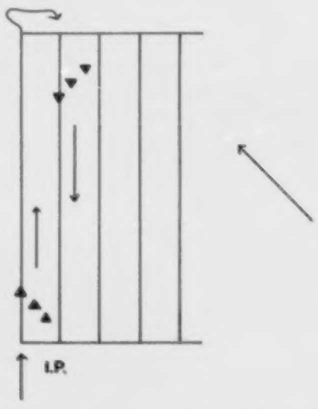

Figure 2. Spray block showing initial point relative to wind direction.

accurately. The lead pointer, flying two to three miles ahead likewise endeavors to be above the line-end at the same time as the spray team to radio "booms-off" accurately. In the remote Crown and industrial holdings to which TBM's are restricted, spray lines are limited to a maximum of 8 to 10 miles (13 to 16 km) because of the inability of the slower pointers at 90 knots to accomplish this task over longer distances.

Upon completion of the first "pass," No. 2 pointer establishes the IP of the second pass, the lead pointer becomes the follower and the spray team reverses direction in the opposite echelon.

Feasibility of Electronic Systems

Apart from its sophistication, the aerial flagman system requires a fleet of pointer aircraft and staff approximating that of the spraying fleet. This additional organizational and cost burden became of increasing consequence as spray programs in New Brunswick escalated in size and complexity during the 1970s and 1980s. As in Quebec and Maine, this created an interest in more technologically advanced spray guidance systems. The Inertial Navigation System (INS) adapted for spraying with multi-engine aircraft in Quebec has been used on infrequent occasions when such aircraft have been used in New Brunswick, but offers little for the future because it is impractical on the smaller aircraft that have become increasingly mandatory.

The need for more exacting navigation has also increased in the past 7 years for environmental reasons, and to accommodate the more selective, discontinuous "targeted" spraying tactics required in part by regulation and in part by forest management directions taken by the New Brunswick Department of Natural Resources. Under regulatory constraints established in 1977 and for other practical reasons, spraying within the one-mile (1.5-km) setback from year-round habitation is limited to smaller agricultural type aircraft. In 1984 this category involved over 500 separate spray blocks ranging in size from 30 to 3400 ha (74 to 8,400 acres). In the more remote Crown and industrial holdings, TBM spraying remains the norm with the recently added complication of greater discontinuity of spray emissions because of stricter exemptions of streams and areas of low vulnerability or commercial value. Taken altogether, these changing tactics have 1) significantly increased the size and organizational complexity of spray and pointer fleets and 2) placed considerable further strain on the adequacy of conventional navigation practice.

Investigation of Electronic Guidance Systems

Active investigation of electronic guidance systems was commenced by Forest Protection Limited in 1978 with a test of the Marinav/Del Norte Flying Flagman. Simulated spray runs were attempted with demonstrator equipment mounted on a Forest Protection Limited Cessna 172. Although tested over relatively even topography, as New Brunswick forests go, the line-of-sight signals proved too weak and erratic at normal spray heights to offer promise for practical use.[1]

In 1979, Forest Protection Limited staff attended several workshops and conferences on Loran C systems, one of which was tested that year by the State of Maine. Since then contacts have been made with at least 10 supplier/developers and several field trials have been run. To this point, these activities have confirmed that the Loran approach, if suitably developed, could offer the best promise and have revealed some of the obstacles to immediate operational application.

A principle advantage of the Loran system is that its low frequency signals are considerably less affected by topography than high frequency line-of-sight systems. Although located essentially for marine navigation, for which the system was originally designed, signals from existing U.S. and Canadian Coast Guard transmitters can readily be used for aerial navigation often several hundreds of miles inland. When first tested for aerial defoliation surveys in New Brunswick in 1980, East Coast coverage was provided by a system of master and slave transmitters located at Nantucket, MA, Caribou, ME, and Cape Race, Nfld. This system proved adequate for flights at about 160 m (525 ft) above the forest for the central and southern parts of the province but not for the north (Knox 1981). This deficiency was expected to be corrected by the addition of an additional transmitter at Fox Harbour, Labrador, in early 1984, but tests to date have yet to receive signals of adequate strength. Tests of one very recently developed Loran C model, however, give promise of being able to correct inaccurate or missing signals in northern areas by cross-tying between the Canadian East Coast Chain of transmitters and one at Seneca, N.Y. on the Northeast U.S. Chain.

The full potential of the Loran system for New Brunswick spray guidance therefore depends to a yet-undetermined extent upon signal coverage over which equipment developers and users have little if any control. However, use of the system for those parts of the province with good signal coverage requires only the requisite equipment adaptation and technology transfer. Ideally, this would provide affordable instrumentation for the types of aircraft now used in New Brunswick and would permit forest managers who are responsible for designing spray plans to have more direct control of targeting precision. The equipment must be capable of in-flight operation by the spray pilot alone and be programmable in advance for navigation to initial points of intended spray lines, accurate track-ing along them, and boom control where reliance on pilot or pointer judgment is unreliable or impossible. By accepting suppliers' claims that all of this is technically possible now, the spray manager's problem appears to come down to the job of competent programming. It is demonstrably possible now to direct aircraft to given map coordinates, to track given magnetic courses, and signal boom operation with excellent repeatability, e.g., for second applications. However, prespray trial and error calibration is essential for each spray block because it is not possible to guarantee that the coordinates entered and intended geographical location are identical to within a few metres. In short, as with all programmable instrumentation, a reliable result depends upon careful, time-consuming and expensive preparation by highly skilled technicians. Until autopiloting becomes feasible it must also depend upon pilots who are highly skilled in instrument flying as well as in the other aspects of forest spraying.

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[1] Jewers, L.H. 1978. Forest Protection Limited File Report.

Forest Protection Limited intends to continue its investigation of new developments in the adaptation of the Loran system and to the extent that it can, to help foster such development. At this point, it would appear that major questions exist as to industrial incentive for development of such specialized Loran application and from what sources the necessary underwriting should be provided.

Literature Cited

Flieger, B.W. 1964. A new method for guiding spray aircraft. Can. For. Serv., Ottawa, Ont. Bi-monthly Prog. Rep. 20 (1):2-4.

Knox, S. 1981. Aerial evaluation of damage from spruce budworm attack in New Brunswick: new methodology — 1980 Tech. Rep. 80/T/3 Forest Protection Limited, Fredericton, N.B.

Discussion Group C —
Applications Technology

Considerations in Timing Insecticidal Sprays on Different Host Trees of the Spruce Budworm

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Our basic data were derived from repeated observations (every 48 hours) on individual caged spruce budworm larvae on branch tips of balsam fir, white spruce, red spruce, black spruce, and hemlock (Hansen and Dimond 1982). Phenomena found to relate to timing sprays were the timing of budbreak and new shoot elongation in different host tree species, persistence of bud caps that shelter larvae from sprays in some hosts, sizes of buds and shoots on different hosts, and the behavior of larvae as it influences the likelihood that they will encounter spray droplets. Interacting with these factors is abundance of the budworm.

The major concern for budworm abundance results from the ability of larvae in bud-mining stages to destroy with little feeding the total potential of a bud to produce a shoot. When budworm larval populations approach one or more per bud, severe damage is likely to have occurred before buds break. Under these conditions, one uses split applications of sprays with the first treatment applied just before or during the bud-mining stage. Heavy kill of insects is not expected in the first application because of the protected nature of miners within buds. However, some bud mining can be avoided, and if the second application is applied when larvae are well exposed in expanding shoots, substantial reduction in larval numbers is achieved.

When larval numbers are more moderate, damage through bud mining remains a problem on red spruce, black spruce, and hemlock, but the problem is reduced on fir and white spruce. This reduction in the latter is due to their early budbreak and rapid spring growth. We found that bud mining was complete on fir and white spruce by May 20, on hemlock by May 26, and on red spruce and black spruce by June 6 (Hansen and Dimond 1982). These dates corresponded with budbreak on the five host species in that year.

The result of the extended bud-mining period on trees of late phenology was that twice as many buds per larva were mined on red spruce (2.3) as on fir (1.0) or white spruce (1.2). In addition, of buds that were attacked, 56 percent survived to become shoots on fir, 33 percent survived on white spruce, and 13-16 percent survived on red spruce and black spruce. Only 7 percent of attacked buds on hemlock survived, but this is related more to the small size of hemlock buds than to delays in budbreak.

It is apparent from the paragraph above, that with moderate budworm populations, most buds of fir and white spruce will survive beyond the budbreak stage. A single application of spray applied after budbreak will find the insects exposed to spray droplets and highly vulnerable, and may be all that is required for satisfactory protection. On white spruce, the proper timing is later than on fir because of the protective bud scales that persist on the tip of the expanding shoots. Where both host species are common in a stand, split applications are appropriate with the first timed for fir and the second for white spruce.

High levels of bud mortality due to budworm feeding are more common on red spruce and black spruce. The spray manager must attempt to reduce this impact or little benefit will be achieved from spraying these hosts. Our data suggest one early opportunity for spraying spruce.

Table 1
Locations of spruce budworm larvae on different hosts

	Location of larvae	
Host	*Within buds*	*Outside buds*
White spruce	*85%*	*15%*
Balsam fir	*78%*	*22%*
Hemlock	*67%*	*33%*
Red spruce	*48%*	*52%*
Black spruce	*56%*	*44%*

The observations (Table 1) were made at the time that buds on fir and white spruce had swollen appreciably, showing some green color through the bud scales, but had not yet broken. Buds on the other hosts showed no swelling. Needle mining stages had been completed. A trend of greater exposure of larvae with later spring phenology of the hosts is suggested.

Our explanation for the result in Table 1 is that, having completed needle mining, larvae are delayed in entering buds on trees where buds have not swollen to some extent. More information is needed on the precise timing of this occurrence and on its duration. It should be the timing of a first application of sprays on red spruce, black spruce, and their hybrids. The second application should be delayed until buds are broken and bud caps fallen.

Literature Cited

Hansen, R.W.; Dimond, J.B. 1982. The feeding biology of spruce budworm on several hosts with reference to timing of insecticidal sprays. Maine Agr. Exp. Sta., Univ. ME., Orono, ME. Misc. Rep. No. 266.

Discussion Group C —
Applications Technology

Spray Technology — The Biological Interface

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The goal of the sprayer — low-cost protection of foliage — is achieved by distributing insecticide droplets of optimal potency in numbers appropriate to the spruce budworm larval distribution pattern, at a time most favorable to larval contact with residues. Because the larvae are well concealed, they are not the prime target for droplet impingement; rather the aim is to deposit droplets at sufficient density on the exposed foliage at the perimeter of potential larval habitats. The biological interface is the relationship between droplet distribution and the biological characteristics of insect and tree which influence toxic contacts.

Studies have been conducted at the Maritimes Forest Research Centre from 1981 to 1984 on: 1) Identification of deposit needed to attain a given percentage mortality (optimal droplet size and density, heterogeneity of deposit, receptivity of various foliage classes, toxic persistence of deposits); 2) Toxicology: the mode of entry of insecticides into budworm larvae; measurement of sublethal toxicity; 3) The effect of timing (larval development, bud/shoot growth, population density and damage reduction); 4) Larval vulnerability relative to post-spray weather (movement, silking behavior, feeding); 5) Definition of effective swath width and influence of drift.

These field studies represent a detailed documentation of seven sprays of fenitrothion emulsion formulation applied in ultra low volume (ULV) by single-engined aircraft (Grumman TBM, Cessna 188); they focus on a comparison of the budworm responses on balsam fir and red spruce in the same stands.

Deposit

Deposit patterns, using the single shoot as the basic sample unit, have been measured across a spatial array: across stand, across swath, through crown depth, per tree, upwind *vs.* downwind aspects, among branches, and among shoots. Characteristically there was high heterogeneity, with gradients of deposition downwind and through the crown, such that a significant percentage of the budworm population was not at hazard due to low deposit. This is partly inherent in the filtering structure of the canopy, and the wind gradients with height above ground. The density of droplets is largely a function of the diameter spectrum. The effective droplets were in the 10-30 microns class (evaporated formulation); droplets <10 microns, abundant at emission, were rarely detected on foliage, whereas droplets >30 microns — although incorporating most of the spray mass — were too sparse to be effective. Sprays varied widely in efficiency of the deposit; an attempt to explain this variation in terms of meteorological parameters is being made.

Toxicology

The relationship between spray deposit pattern and mode of entry into larvae is of primary importance; the candidate modes are direct dermal impingement, dermal contact with residues by locomotion, ingestion of residues at site, systemic movement of residues to the feeding site, and tracheal absorption of insecticide vapor. Current studies are investigating the toxic potentials of vapor emanation and systemic movement. Prima-facie evidence implicates dermal contact with residues as the most promising hypothesis. Field studies have shown that a significant part of the larval fallout results from sublethal toxicity.

Timing

Red spruce (late flushing) and balsam fir (early flushing) present quite different targets during the spray season. In some sprays, the responses of budworm populations resident on fir varied markedly from those on spruce. Timing is a function of larval instar (susceptibility curve) and host-specific behavioral differences in exposure to residues. The criteria for optimal spray timing are so far undetermined, but an understanding of vulnerability mechanisms is emerging.

Vulnerability

Post-spray weather is a factor of efficacy. Deposits persist several days, and it is hypothesized that larvae make contact with residues as a result of movement around the habitat perimeter to spin silken defenses. Silking is stimulated by favorable weather (warm, calm, dry), which is therefore conducive to increased efficacy. Movement is inhibited by cold weather (induces torpidity) and by wet or windy weather (unfavorable to silk attachment) so contact with residues is reduced.

Swath Width and Drift

A drop-tray method has been found useful for determining efficacy in terms of larval fallout. Experiments in 1981 showed budworm response to drift to 1200 m (3,937 ft) downwind. Experiments in 1983 and 1984 have documented the gradient of efficacy across a 400 m (1,312 ft) swath, with a view to exploring the possibility of expanding the current nominal widths.

Discussion Group C — Applications Technology

Spectrum and Atomization

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The initial drop size spectrum produced by a spray system is a key factor that affects the spray deposition and coverage in the target area as well as the fraction of spray that may drift out of the area. The atomization process is complex and the drop size distribution is affected by a multitude of variables, such as nozzle design, pressure, flow rate, air velocity, orientation angle, and fluid properties.

Unfortunately, the measurement of the drop size spectra from agricultural aircraft poses many problems that may introduce errors. Most techniques may introduce errors because of truncation of relatively large numbers of drops produced below detectable size, truncation above maximum size class, and potential drop interference and/or bias in sampling technique. The *in situ* laser techniques have greatly reduced some of the measurement errors, but some limitations may still persist and should be recognized.

The objective of this report is to summarize some of the results of drop size spectra obtained from typical spray systems used for aerial application of materials for control of spruce budworm.

The particles were measured *in situ* in the airstream by means of a digital drop image analyzing system (Particle Measurement System, OAP-2D-GA1 laser probe and PDPS 11-C computer system). The particles are classified into 62 size classes with a detection limit from 23 to 2062 microns. An x-y positioning system was used to mechanically scan the entire spray pattern. Nozzles were tested in flight with a De Havilland Beaver aircraft and in a wind tunnel with a 61 × 61 cm (24 × 24 in) cross section.

A systematic series of flat fan, hollow cone and rotary atomizers were evaluated. Four types of fluids were tested; water, a water-diluted suspension of *Bacillus thuringiensis* (B.t.), a water diluted emulsifiable suspension of B.t. and a cottonseed oil base spray with an insecticide.

Figure 1 illustrates results from 80° flat fan nozzles operating at 276 kPa (40 lb/in^2) in a 161 km/hr (100 mph) air velocity. As shown an increase in nozzle angle relative to the airstream reduces the volume median diameter, D_{V5}, and an increase in flow rate by increasing size of nozzle (keeping a constant pressure) increases the D_{V5}.

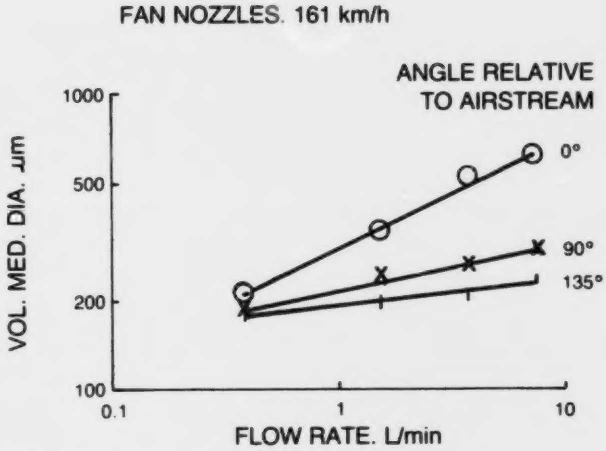

Figure 1. Effect of flow rate and nozzle orientation angle of $D_{v.5}$ for flat fan nozzles at 161 km/h and 276 kPa.

Table 1 contains a summary of drop spectra for a variety of test conditions. In general the cottonseed oil and B.t. spray mixtures produce a slightly smaller D_{v5} than a water spray. Flat fan and hollow cone nozzles can be selected to give somewhat similar drop size spectra. The rotary atomizers can produce a smaller D_{v5} than the typical fan and cone nozzles. The largest drop size spectrum was produced with a large flat fan nozzle at 0° angle to the airstream. The Relative Span indicates the relative uniformity of drop spectra and is similar for all types of nozzles tested.

Table 1
Summary of drop size from various nozzle types and fluids at an airspeed of 161 km/h and 276 kPa

Nozzle type	*Nozzle angle Degrees*	*Flow rate/noz. L/min.*	*Type form.*	$\overline{D}_{30}$* μm	$D_{V.5}$* μm	*Range of* drop size* μm	*Relative* span*
Flat fan 8001	*135*	*0.38*	H_2O	*108*	*181*	*97-258*	*0.89*
8004	*0*	*1.5*	H_2O	*188*	*334*	*167-602*	*1.30*
	90	*1.5*	H_2O	*137*	*242*	*129-366*	*0.98*
	135	*1.5*	H_2O	*134*	*202*	*125-298*	*0.85*
	135	*1.6*	*CSO**	*101*	*188*	*84-292*	*1.10*
	135	*1.5*	*Thur**	*117*	*189*	*107-276*	*0.89*
	135	*1.5*	*Dipel**	*108*	*181*	*100-255*	*0.86*
Hollow cone D2-23	*90*	*0.38*	H_2O	*124*	*193*	*109-279*	*0.88*
D4-45	*90*	*1.4*	H_2O	*135*	*223*	*131-333*	*0.90*
Micronair® (8000 RPM)		*11.4*	H_2O	*97*	*118*	*56-179*	*1.04*
Beecomist® (8350 RPM)		*11.4*	H_2O	*114*	*178*	*113-270*	*0.89*

*CSO = cottonseed oil
Thur = 12 BIU Mixture of Thuricide and water
Dipel = 12 BIU Mixture of Dipel and water
*$\overline{D}_{30}$ = Volume mean diameter
*$D_{V.5}$ = Volume median diameter
*Range = Range of drop diam that contains 80% of spray volume
*Relative Span = $\frac{\text{Range}}{D_{V.5}}$

Discussion Group C —
Applications Technology

Droplet Spectrum Measurement by Laser Probe Methods

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A laser light scattering probe and a laser droplet imaging probe were used to measure the droplet emission spectrum of various commercial aerial spray atomizers. The light scattering probe (a PMS FSSP probe) was recalibrated using glass beads and the Mie equations were solved to provide calibration curves for a range of refractive index and light absorbance (Bontemps 1983). The range of droplet size measurable with this device is from 0.5 to 55 microns. The light imaging probe (PMS OAP-260X) has a nominal range of 20 to 600 microns, and functions by projecting the shadow of the droplet onto a strip of discrete photodiodes which are read and the digital data converted to droplet diameter.

Measurements were done in the NRC 10 × 20 (ft) wind tunnel in Building M-46 on Montreal Road in Ottawa. The tunnel has a 40-foot long test section which was equipped with a venturi-type flow restrictor to increase its maximum speed to 170 mph (76 m/s). This permitted measuring of atomizer characteristics at actual aircraft operational speeds. The probes were mounted so that their sample volumes were approximately 1.5 m (5 ft) downstream of the atomizer. A traversing system was used to permit detailed analysis over the full cross-section of the spray plume. The tunnel air flow was laminar in all cases. Droplet evaporation was negligible for droplet sizes down to 10 microns for volatile formulations (in this case, water or methanol-water solutions), but was probably significant at smaller sizes. Measurements much closer to the atomizer are subject to errors because the droplet break-up mechanism requires about a 0.5 m (18 in) fetch downstream of the atomizer to be complete.

The commercial atomizers studied included the Teejet® 11010 flat fan nozzle, the Micronair® AU 3000 rotating basket atomizer, and the Beecomist® 360 rotating porous sleeve atomizer (porous polyethylene sleeve with 40 micron diameter pores).

Results and Discussion

The probe output data were first tested by applying the mass balance criterion, i.e., the flow rate of liquid into the atomizer equals volumetric flow rate of droplets out. After considerable analysis it was found that the OAP-260X probe gave consistently much higher droplet flow rates than were supplied to the atomizer. This has been attributed to "coincidence error," that is, the device is designed as a single-droplet measuring device, and when two or more droplets are present at one time in the sample volume, the droplet diameter reported is the sum of the two distinct diameters present in the sample volume. Resulting volume calculations are therefore erroneous. Data from this probe could not be used. Instead, previously obtained (Tomney 1978) photographic data at greater than 50 microns were used to add on to the valid data from the FSSP probe (0.5 to 55 micron range) to provide the complete spectrum.

Results can be summarized as follows:

1) The numbers of small droplets generated increases as diameter approaches zero, down to at least 2.0 microns, in contradiction to the predictions of the widely accepted Nukiyama-Tanasawa distribution functions (Tomney 1978).
2) The Beecomist® 360 with a 40 micron polyethylene sleeve at 13 volts in an air flow of 40 m/s with 1.2 L/min of water generated 97 percent of its spray volume between 15 and 50 microns.
3) The Micronair® AU 3000 at 11.4 L/min of water, air flow of 47 m/s using 13.5 inch blades at 25°, generated 73 percent of its volume in the 30 to 100 micron band.
4) The Teejet® 11010 nozzle at 3.8 L/min of water at 67 m/s of airflow generated 34 percent of its volume between 30 and 100 microns.

In general, the usual spectrum statistic of average droplet size is of no utility in describing the spectrum for aerial spraying purposes because of the very large number of very small droplets. A new approach is required, e.g., the mass fraction of droplets in the optimum size range for the particular target, and the mass fraction in the size range for off-target drift.

The results with respect to small droplet generation are well borne out by measurements on the off-target drift cloud from aerial spray field trials reported by Crabbe et al. (1983) for droplet sizes below 20 microns. An additional field trial result (Kristmanson and Picot 1983) is that the optimum droplet size range for best spraying efficacy for spruce budworm control is between 15 and 50 microns delivered to the foliage. An examination of the above data shows that with an evaporation factor which causes about 50 percent reduction in diameter of the emitted droplet, provided viscosity and surface tension differences are not too great for formulations compared to water, the Micronair® produces twice as much mass of fluid in the right droplet range as does the Teejet® (under the conditions of measurement). On the other hand, the Beecomist® could be fed with concentrated nonevaporating insecticide and could generate three times the mass in the required delivered droplet size range based on the same feed rate (more atomizers would be required).

Additional experiments have been conducted to characterize atomizer performance, such as the effect of changing the wind speed, the atomizer rotational speed, and the properties of the fluid. In general, increased speed decreases droplet size, as does a reduction in droplet surface tension. Increased viscosity tends to increase droplet size. No general correlation is available as yet to describe atomizer performance. Additional data is available in the M.Eng. thesis by Bontemps (1983).

Literature Cited

Bontemps, X. 1983. The optimization of aerial spray atomizers. M. Eng. Report., Chem. Eng. Dep., University of New Brunswick, Fredericton, N.B.

Tomney, T.D. 1978. Drop size distributions in aerial spraying. M. Eng. Report., Chem. Eng. Dep., University of New Brunswick, Fredericton, N.B.

Crabbe, R.S.; Elias, L.; Davie, S. 1983. Field study of the effect of atmospheric stability on target deposition and effective swath widths for aerial forest sprays in New Brunswick. Part II. National Research Council of Canada, Ottawa, Ont. Report LTR-VR-65.

Kristmanson, D.D.; Picot, J.J.C. 1983. Dunphy Drift Trials — 1982. Chem. Eng. Dep., University of New Brunswick, Fredericton, N.B.

Discussion Group C —
Applications Technology

Summary

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The modern era of spray technology has been slow in coming. The obvious mental comparison between spray droplets and raindrops that people intuitively make has stunted the development of the science. Even after Himel and Moore in 1967 demonstrated that droplets actually observed on conifer foliage represent only the small end of the emitted size range and concluded that 90-95 percent of the applied insecticide was wasted in large drops, the recognition of the importance of spray physics as a basis for spray technological development was slow.

In recent years, however, increasing acceptance by managers and operators of this concept has spurred the research effort. Simultaneously, the development of new technologies such as laser droplet spectrometers and electronic guidance systems has enabled us to make essential measurements which were hitherto virtually impossible. The realization that aerial spraying produces a relatively sparce deposit of very small droplets in the larval microhabitat has also led to the need to understand, in great detail, the behavior of the target larvae and the influence of weather, host species, and host and larval development on that behavior.

Although much progress has been made, much remains to be done. The single greatest problem facing this type of research is the massive variation introduced by the complex interaction of physical, biological and meteorological parameters operating in a highly heterogenous framework — the budworm-prone forest. A second caveat that must be faced by manager and scientist alike is that solutions devised through research will not solve all operational problems. The recommendations of the scientist will not always be operationally feasible. Constraints placed upon the operator by weather, fleet size, spray window and budget may often preclude his acting upon the scientist's advice. Nevertheless, if aerial insecticide application is to survive as a viable and socially acceptable forest management tool, it is essential to continue to improve our understanding of the entire spray efficacy process.

Discussion Group D —
Environmental Impact
Assessment

Environmental Impact Assessment Relevant to Spruce Budworms and their Control

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Forest management in its broadest sense implies managing forest areas so as to optimize a variety of economic, social and aesthetic values required by different user groups. Forest areas represent far more than simply sources of lumber and fiber — they provide wildlife habitat, support recreational opportunities such as hunting, fishing and camping, and stabilize and contribute to the quality of water, soil, and air. Management of spruce budworms, an important aspect of forest management in much of our forest area, must be done with due regard to the multiple uses of our forest land base and full consideration of the impacts the budworm or our techniques for controlling its impacts have on other components of forest ecosystems.

Throughout the CANUSA Program, there has been considerable activity in assessing such impacts. Many of these activities, including some initiated with CANUSA funding, have evaluated the impacts of spruce budworm control agents, particularly chemical insecticides, on nontarget organisms ranging from forest songbirds and small mammals to algae and microbes. Much of the work has evaluated the impacts associated with new commercial products or formulation components. This has led to the selection and use of chemical control options posing less hazard to forest communities than previously used materials. CANUSA-initiated research on biological control strategies, particularly those based on commercial *Bacillus thuringiensis* preparations, has resulted in reduced reliance on chemical insecticides for operational spray programs, further decreasing environmental impact associated with them.

Meetings of CANUSA environmental impact working groups spent much time discussing environmental monitoring of budworm control programs, both the methods employed and results obtained as well as from the perspective of their usefulness in influencing control policies and spray program planning. Most provinces and states have had some form of environmental monitoring committee, and many have progressed from widespread monitoring of forest communities in large operational spray programs to more limited and basic ecological studies in selected areas, experimental spray blocks, or laboratory situations. It appears most jurisdictions have had difficulty sustaining impact studies addressing management-oriented questions, or have concluded that sufficient information on spray impacts is currently available to limit the utility of further monitoring work, especially now that the "harder" chemical insecticides have had their use curtailed or severely limited. Methods for conducting insecticide impact studies have been developed for many groups of organisms and forest environments, and are readily available for use (e.g. Adamus 1983; Kingsbury 1984).

One area of environmental impact assessment still in need of development is looking at spruce budworm management in the context of overall forest management, putting emphasis on evaluating habitat changes resulting from long-term impacts of the budworm and programs controlling the insect. Destructive effects of the budworm itself, or silvicultural activities aimed at managing stands so as to address the problems of budworm attack, both result in habitat modification which can impact on wildlife. The forest manager needs to identify the potential environmental effects of whatever forest management strategies are chosen to deal with the budworm, whether they include the use of chemical or biological insecticides, application of silvicultural techniques, or nonintervention and reliance on salvage activities. Technology transfer activities during the CANUSA Program have served to partly fill this need (e.g., Bart and Hunter 1978; Peakall and Bart 1983; May 1984; Oliveri 1984; Trial 1985). This information should then be applied in the planning phase of budworm management to predict conflicts between strategies chosen to deal with the budworm and the protection of environmental values within the area (Trial and Kingsbury, 1984). For example a nonintervention strategy may result in the loss of critical deer wintering habitat, and may require modification of plans to protect such areas by selected use of insecticides. In most instances impacts can be minimized to an acceptable level by careful selection of management options and implementation of mitigating techniques, such as establishing spray buffers around sensitive areas or limiting the size or continuity of areas treated with a given silvicultural practice. In this fashion we can manage the budworm while giving due consideration to the protection of all the values present within the threatened forest areas.

Literature Cited

Adamus, P.R. 1983. Techniques for monitoring the environmental impact of insecticides on aquatic ecosystems. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 613, 64 p.

Bart, J.; Hunter, L. 1978. Ecological impacts of forest insecticides: an annotated bibliography. New York Co-operative Wildlife Research Unit. Ithaca, N.Y., 128 p.

Kingsbury, P.D. 1984. Environmental impact assessment of insecticides used in Canadian forests. Pages 365-376 *in* W.Y. Garner and J. Harvey, Jr., eds. Chemical and biological controls in forestry. Am. Chem. Soc. Sympos. Ser. 238. Washington, D.C.

May, T.A. 1984. Insecticide impacts on non-target terrestrial biota and their relevance to forest pest management. University of Maine, College of Forest Resources, Orono, ME. Tech. Note 89. 109 p.

Oliveri, S.F. 1984. Assessment of the environmental impacts of spruce budworm suppression operations in Maine and eastern Canada. Trans. N.E. Fish and Wildlife Conf. 40:31-40.

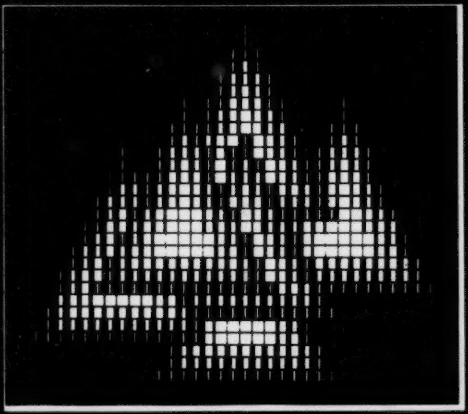
Peakall, D.B.; Bart, J.R. 1983. Impact of aerial applications of insecticides on forest birds. CRC Critical Reviews in Environmental Control 13(2):117-165.

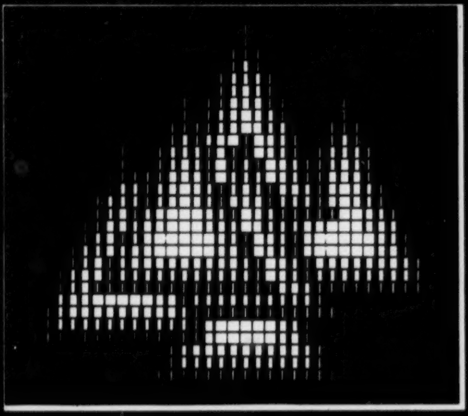
Trial, J.G. (In press). Environmental monitoring of spruce budworm suppression programs in the Eastern United States and Canada: an annotated bibliography, Maine Agricultural Experiment Station, Orono, ME.

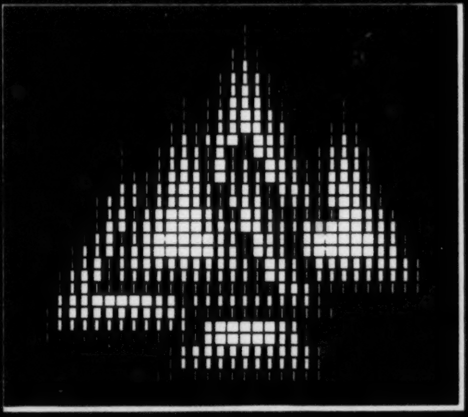
Trial, J.G.; Kingsbury, P.D., 1984. Spruce budworm management planning — Limiting environmental impacts. Pages 133-140 *in* D.M. Schmitt, D.G. Grimble and J.L. Searcy, eds. Managing the spruce budworm in Eastern North America. U.S. Dep. Agric., Washington, D.C. Agric. Handb. 620.

Part IV

Integrated Forest and Pest Management; Implications for Forest Management







Progressing Toward Integrated Pest Management of the Spruce Budworm in the Eastern United States

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Integrated pest management (IPM) as it applies to forestry consists of a philosophy, concepts, and methodology. IPM is based on principles of ecology; methodology involves a combination of tactics aimed at suppressing populations; the goal of IPM is to maintain populations of damaging organisms at tolerable levels based on economic, ecological, and social values; and IPM is a component of total resource management. The conceptual framework and components of IPM include: pest population dynamics, treatment tactics, impact on values, and benefit-cost integration. The methodology of IPM includes decision-making to allocate forest management resources and the actual tactics used in the forest to alleviate the negative impacts of pest populations. In the ideal program, the decision-making process for spruce budworm involves strategic planning over the long term, long-term decision-making, and short-term decision-making. Long-term, forest-directed decisions are made to prevent an outbreak from causing significant damage to the forest. Short-term decisions are responses to threatening population upsurges of budworm and use tactics directed at the insect. Long-term and short-term decision-making often are combined when infestations and outbreaks do not subside appreciably. IPM tactics include: doing nothing, insect-directed efforts, and forest-directed efforts.

IPM programs have been developed and implemented in the United States since about 1970. National programs were funded by federal agencies, and such funding was aimed at both research and extension. Through federal agency commitment and public laws, IPM received much impetus during 1971 to 1980. Regional IPM programs in agriculture including research, extension, and teaching were established in 1979. Many statewide IPM programs in agriculture have existed since 1972.

Spruce-fir forests in Minnesota, Wisconsin, Michigan, New York, Vermont, New Hampshire, and Maine experience infestations and outbreaks of spruce budworm. Each state, through a state natural resources management agency, has adopted an IPM philosophy for dealing with forest pests. Six states have IPM programs for spruce budworm. The methodology used by each depends in part on ownership and in part on the intensity of forest management efforts.

Considerable IPM methodology was developed during the CANUSA Program for application in various states and for a variety of specific circumstances. IPM methodology useful in decision-making includes: damage assessment, hazard rating, site classification, population monitoring, economic decision-making, computer-based planning and decision models, growth and yield models, wood utilization models, needs assessment surveys, silviculture selection models, and many others. IPM tactics that may prove useful include: *Bacillus thuringiensis*, chemical pesticides, strip cuts, shelterwood cuts, targeted harvesting, mixed wood management techniques, and many

more. Examples of IPM methodology are reviewed and the implementation process is assessed. Use of various methodologies varies by state, depending on the value of spruce-fir and the intensity of spruce-fir management.

La lutte intégrée dans le contexte forestier représente une théorie, un ensemble de principes, un mode d'action. Elle met en application les principes de l'écologie. Elle consiste à combiner diverses techniques afin de réprimer les populations de ravageurs. Son but est de maintenir ces populations à des niveaux tolérables compte tenu des valeurs économiques, écologiques et sociales. La lutte intégrée constitue un aspect de la gestion globale des ressources. Ses considérations et préoccupations portent notamment sur la dynamique des populations de ravageurs, la dynamique des peuplements forestiers, les tactiques de traitement, les répercussions et les rapports avantages-coûts. Ses méthodes comprennent la prise de décisions concernant l'affectation des ressources de gestion des forêts et les tactiques employées en forêt pour atténuer les effets négatifs des populations de ravageurs. Dans un programme idéal de lutte contre la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]), le processus de prise de décisions comporte la planification de stratégies à long terme et la prise de décisions à long et à court termes. Les décisions à long terme portant sur la forêt visent à prévenir une destruction importante de celle-ci qui serait causée par une pullulation, tandis que les décisions à court terme sont prises pour répondre à une hausse menaçante des populations de la tordeuse et utilisent des tactiques dirigées contre l'insecte. Les prises de décisions à long et court termes sont souvent combinées lorsque les infestations et pullulations ne s'effondrent pas de façon appréciable. Les tactiques de lutte intégrée comprennent le laisser-faire, les efforts dirigés contre l'insecte et les efforts portant sur la forêt.

Aux États-Unis, des programmes de lutte intégrée sont conçus et mis en oeuvre depuis 1970 environ. Des programmes à l'échelle nationale ont été financés par des organismes fédéraux, le financement portant sur la recherche et la diffusion. Grâce à l'engagement des organismes fédéraux et aux lois publiques, la lutte intégrée a reçu beaucoup d'appuis au cours de la période de 1971 à 1980. Des programmes régionaux de lutte intégrée en agriculture comportant recherche, diffusion et formation ont été établis en 1979. Beaucoup d'États possèdent de tels programmes depuis 1972. Les forêts d'épinette et de sapin (*Picea* spp. et *Abies* spp.) de sept États (le Minnesota, le Wisconsin, le Michigan, le New York, le Vermont, le New Hampshire et le Maine) ont été touchées par des infestations et des pullulations de la tordeuse des bourgeons de l'épinette. Tous ces États, par l'intermédiaire d'un organisme de gestion des ressources naturelles, ont adopté la démarche de la lutte intégrée contre les déprédateurs des forêts. Six des sept États touchés ont un programme de lutte intégrée contre la tordeuse des bourgeons de l'épinette. Les moyens employés par chacun peuvent cependant varier en fonction de la propriété des terres et de l'intensité des efforts de gestion des forêts.

Un savoir-faire considérable en lutte intégrée applicable à divers États et à une gamme de situations déterminées a été acquis au cours du programme CANUSA. La méthodologie utile pour la prise de décisions inclut l'évaluation des dommages, l'analyse des risques, la classification des emplacements, la surveillance des populations, la prise de décisions économiques, la planification assistée par ordinateur, l'utilisation de modèles, notamment pour

les décisions, la croissance et la production, l'utilisation du bois et la sélection sylvicole, ainsi que l'étude des besoins. Les tactiques qui peuvent s'avérer utiles comprennent les épandages de *Bacillus thuringiensis* et de pesticides chimiques, les coupes par bandes, les coupes progressives, les coupes d'arbres individuels, les techniques de gestion d'essences mélangées et beaucoup d'autres. Des exemples de démarches de lutte intégrée sont examinés, et le processus de mise en oeuvre est évalué. Les démarches choisies varieront d'un État à l'autre suivant la valeur de la forêt de sapin et d'épinette et l'intensité de la gestion.

Introduction

Philosophy of IPM

Integrated pest management or IPM as it applies to forestry is really a new name tagged to many of the existing practices that foresters term "forest management." Indeed, Davis (1954) used the term "integrated" when referring to the large array of disciplines, including insect and disease management, that are practiced in forestry. In our view, the very roots of current integrated pest management can be traced to the philosophy and practice of forest management — which is to ensure the availability of forest benefits in the quantity and quality required, at the location required, and in a timely manner appropriate for their use (Baskerville and Montgomery 1983).

The term "integrated pest management" has evolved to denote a renaissance in pest control philosophy and action, particularly in agriculture. Over the past 25 to 30 years, pest control has changed from the calendar application of DDT to a much more sophisticated and ecological approach requiring monitoring of pests, natural enemies, and damage; projection of events into the future, often involving mathematical models and computers; economical decision-making that considers a variety of actions including no action; and post-action evaluation.

We in forest management have never quite had the same economic latitude for pest control that our counterparts in agriculture have had. In addition, the level of damage we can tolerate in forest management is usually many orders of magnitude greater than what can be allowed in agriculture. Anything short of tree mortality may be permissible for us, and, in some instances, when salvage logging is an option, even tree mortality is tolerated. In general, this has kept forest pest control heavily based on ecological and economic considerations. The IPM programs incorporate several principles to deal with pests in economically efficient yet environmentally sensitive ways (Simmons et al. 1984):

1. **The presence of a pest species does not necessarily justify control action**. In agriculture this has been a hard lesson to learn. But in forest management it has been a historic, common practice, based, in part, on the idea that managers would not spend more money to obtain control than the value of the product they are attempting to protect from damage.
2. **The ecosystem is the management unit of which pests are a small part**. The lessons of silviculture have established centuries of traditional appreciation of the dynamic nature of forests. Most foresters recognize that changes imposed by cultural practices influence a myriad of components in the forest ecosystem, and although we may not be able to comprehend the full complexity of dynamic change, foresters do realize that an intricate complex can exist.
3. **Use and protection of natural enemies is encouraged**. In agriculture, the "magical cure" of pesticides led to indiscriminant and uninformed use that harmed natural enemies necessitating the continued use of pesticides to protect crops from damage. In forestry, even under the most extreme circumstance, pesticide use on a per-acre basis has been at very low volume with infrequent repetition in successive generations of a pest population. The choice of pesticide and the timing of application have most often been done to minimize impacts on natural enemies of the pest.
4. **Any control technique could have unexpected or undesirable side effects**. In agriculture, historic reliance on pesticides resulted in discovering the "three r's" of pesticide usage: *resistance* of pest populations to the pesticide and related pesticides, *resurgence* of secondary pests after natural enemies were reduced, and *residues* of undesirable and sometimes dangerous chemicals in the environment. Thus, evaluation of actions is a requisite for a comprehensive management program. The mensurational aspects of forest-stand management have long institutionalized this principle in forest management.

5. **An interdisciplinary approach is essential**. In agriculture, interdisciplinary work is often difficult as scientists are specialized in subdisciplines that often have no common background in agricultural production. Developing interdisciplinary teams that communicate well is difficult individually and administratively. By contrast, forest scientists, especially those at universities, often have similar backgrounds with specialization at the graduate level. They are often housed under one roof and administered by the same individual(s). Thus, it is easier to find common ground and easier to develop formal and informal interdisciplinary teams.

By definition, IPM is:

> ...an ecologically based pest control strategy that relies heavily on natural mortality factors such as natural enemies and weather and seeks out control tactics that disrupt these factors as little as possible. IPM uses pesticides, but only after systematic monitoring of pest populations and natural control factors indicate a need. Ideally, an integrated pest management program considers all available pest control actions, including no control action, and evaluates the potential interaction among various control tactics, cultural practices, weather, other pests, and the crop to be protected (Flint and van den Bosch 1981).

This general definition comes from an introductory text of pest management and reflects an agricultural bias. IPM as it applies specifically to forestry includes the principles of the above definition but has a more discrete focus. As interpreted by Coulson and Witter (1984), IPM in forest management embodies a philosophy, concepts, and methodology. They point out that the definition of IPM in forestry has evolved over the years but contains four key points: 1) the foundation of IPM is based on principles of ecology, 2) the methodology involves a combination of tactics aimed at suppressing or preventing population growth — several tactics used together constitute a strategy for regulating population growth and abundance, 3) the functional goal of IPM is to reduce or maintain pest populations at tolerable levels based on economic, ecological, and social values, and 4) IPM is a component of total forest resource management. A definition of IPM specific to forestry that captures these four key points was provided by Waters (1974):

> ...integrated pest management is the maintenance of destructive agents including insects, at tolerable levels by the planned use of a variety of preventive, suppressive, or regulating tactics and strategies that are ecologically and economically efficient and socially acceptable. It is implied that the actions taken are fully integrated into the total resource management process — in both planning and operation. Pest management, therefore, must be geared to the life span of the tree crop as a minimum and to a longer time span when the resource planning horizon so requires.

Concepts of IPM

From the definitions provided, one can begin to appreciate the philosophy that undergirds the concepts and methodology of IPM as it applies to forestry. Over the past 15 years, IPM research and application programs have done much to develop IPM concepts as they relate to forest insect programs. Even though research has been conducted on various insects, the conceptual framework and the components contained within it are common. These components include: 1) pest population dynamics and epidemiology, 2) forest stand dynamics, 3) treatment tactics, 4) impact on resource values, and 5) benefit-cost integration. The conceptual framework illustrates how IPM relates to total forest management (Waters and Stark 1980). It further details how complex processes are linked to and influence other component processes. The conceptual framework thus illustrates the kinds of information that would be required to develop a sophisticated forest pest management system. From these components and the interactions between them, seven fundamental principles of IPM in forests are evident (Coulson and Witter 1984): 1) there is a resource in need of protection from pests, 2) insects can periodically become pests through fluctuations in population numbers, 3) the importance of a pest can be judged by its effects on values that are associated with a resource, 4) certain efforts termed "treatment tactics" can sometimes be employed to suppress damaging population numbers, 5) final judgments in IPM decision-making are based on economic criteria — the linkage of IPM to forest management practice, 6) pest management is a component of forest resource management, and 7) data for monitoring pest populations and stand conditions are obtained from various types of forest surveys.

The ideal IPM system would be based on sophisticated knowledge of each of the components and interactions illustrated. In addition, all potential pests of a given forest type and locality would be included in such a system. To date, we have made inroads in developing some of this knowledge for single pest species and their associated forest host types. In practice, no such ideal forest pest management systems exist per se (Waters and Stark 1980), but the framework and concepts that have been developed have been implemented on several insect problems to the extent that our knowledge and abilities will allow. Some excellent examples include the Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunnough)) (Brookes et al. 1978), the mountain pine beetle (*Dendroctonus ponderosae*

Hopkins) (Berryman et al. 1978), and the southern pine beetle (*Dendroctonus frontalis* Zimmerman) (Thatcher et al. 1980), among others.

The Methodology of IPM

The actual implementation of the philosophy and concepts of IPM is embodied in IPM methodology, which can be viewed as two broad categories of human activity: 1) mental processes used in decision-making for the allocation of resources — the information and analysis support system for decision-making in forest management, and 2) the actual tactics used in the forest to attempt to alleviate the negative impacts of pest populations.

IPM Decision Process.

We view IPM as an integral part of forest management, envisioning it as providing a framework for managers to think through problems and visualize possible solutions for the disruptive effects of pests. In this way, IPM is an information and analysis support system for decision-making in forest management. Ideally, it allows the manager to identify current and future pests, their potential impact, possible tactics for minimizing the impact, and repercussions of implementing these tactics. The IPM decision-making model and approach is similar for most forest pests. The specific IPM tactics are more pest-specific and function to execute the IPM decisions.

IPM is implemented through long-term, short-term, and a combination of short-term and long-term decision-making. The broadest decision-making occurs at the strategic planning level. For the spruce budworm, national, regional, and state policies have established IPM as the approach to use. These policies are comparatively long-term and set the stage for subsequent decisions over a shorter time frame and within a smaller geographic area.

Still considered planning, but more restricted in time and space and more specific to detail, is operational planning. These decisions direct specific actions (tactics), timing of those actions, and resource allocation, both human and nonhuman, to achieving an organization's goals. Operational planning encompasses decisions made at the "firm level" — that is, whatever organization set in motion an IPM program, whether public or private, with ownerships of any size that are concerned with forest management.

Within the firm or forest management organization, the stand or small group of related stands termed a "parcel" (compartment) is often the focus of forest management efforts. Here, tactical decisions influence actions on the forest, on the budworm, or both. When management plans are implemented and actions are directed at the forest, long-term "crisis prevention" is the target. A good example of long-term IPM in forest management is the 10-year parcel (compartment) review process used by some forest managers (Simmons et al. 1984). Management objectives are reviewed, often by an interdisciplinary team. Conditions on the site are provided by stand inventory data, maps, and sometimes by on-site visits. Experts representing various multiple-use disciplines — such as management, silviculture, ecology, soils, hydrology, wildlife, recreation, landscape architecture, fire, entomology, and pathology — may make up the team. For example, if they are reviewing spruce and fir stands, they must consider whether damaging spruce budworm populations are likely. If so, they must weigh the probable effects of such populations on the stands. If the populations will influence management objectives negatively, then preventive tactics are sought. Tactics such as abandonment, removal of overmature fir, clearcutting, patch cutting, and selection cutting would be considered. Tactics are then evaluated economically, ecologically, and sociologically. The optimum approach is then the basis for taking certain actions or taking no actions at all. In theory, this is how IPM is incorporated in forest management at the stand level over a long time span (Simmons et al. 1984).

Decisions must be made more quickly when budworm populations are detected or expected to upsurge. We have termed this "crisis response" to indicate short-term decision-making. The crisis results because surveillance and monitoring indicate the probability of damage from spruce budworm populations to be high.

If the prognosis indicates that management objectives would be affected by spruce budworm, then appropriate managers' options (tactics) must be identified. Possible tactics (options) could include doing nothing, presalvage, salvage, or treating with insecticides. Each option has an associated cost and sociologic and ecologic outcomes. The option or combination of options most desirable is then selected and implemented. The outcome is evaluated either during the next surveillance and monitoring or through a special evaluation. Often the process is repeated annually beginning with surveillance and monitoring.

In some portions of the spruce budworm range and during some fairly long time spans, budworm populations do not subside appreciably. In these circumstances, the longer term, stand-directed decisions are combined with the short-term budworm population response decisions; therefore, both long-term and short-term decisions are made simultaneously or in close succession. A flow diagram that depicts how these two processes might operate under ideal circumstances is shown in Figure 1 (from Simmons et al. 1984).

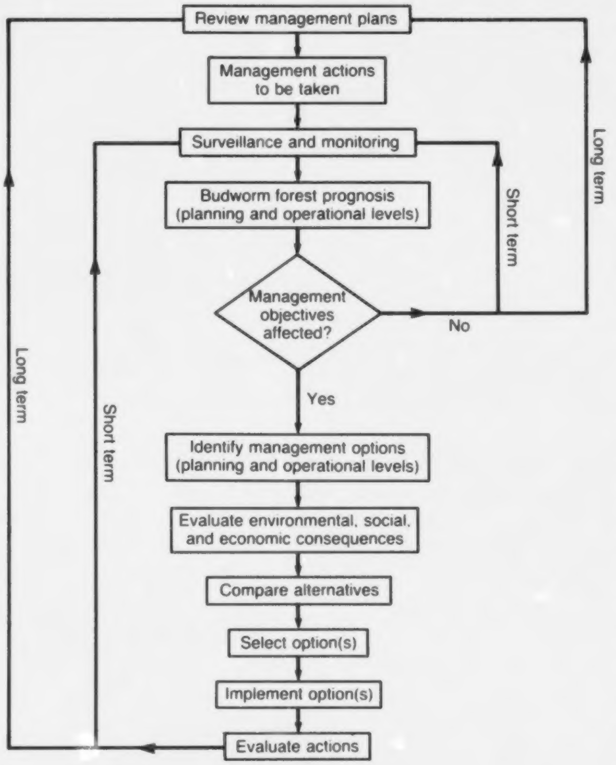
Review management plans
Management actions to be taken
Surveillance and monitoring
Budworm forest prognosis (planning and operational levels)
Management objectives affected?
No
Yes
Identify management options (planning and operational levels)
Evaluate environmental, social, and economic consequences
Compare alternatives
Select option(s)
Implement option(s)
Evaluate actions
Long term
Short term
Short term
Long term

Figure 1. Flow diagram of a hypothetical decision-process that might be used to handle planning, long-term, and short-term decisions (from Simmons et al. 1984).

IPM Tactics

Three broad categories of tactics can be used in combination to form the treatment strategies used in an IPM program: 1) doing nothing, 2) insect-directed tactics, and 3) forest-directed tactics. The do-nothing tactic is usually used where the cost of doing something is unwarranted or environmental and social risks are perceived to be too great to chance taking some action. Insect-directed tactics are those methods that through direct action increase mortality in the insect population. By increasing mortality, we decrease the economic damage to the forest. The primary tools available to use against the spruce budworm are chemical insecticides and the microbial pesticide, *Bacillus thuringiensis* (Table 1). Forest-directed tactics are those that take advantage of the interrelation of forest stand dynamics with pest populations. Ideally, manipulating forest stand dynamics is a way to influence pest population dynamics so that damaging populations of the pest can be prevented. With the spruce budworm this ideal is viewed by many to be extremely difficult or even impossible because of the regional nature of budworm outbreaks. Instead, forest-directed tactics are generally viewed as a way to decrease the amount and intensity of economic damage when an outbreak occurs. A wide variety of forest-directed tactics have been conceived and used by foresters, experimented with by researchers, or both, to deal with the spruce budworm and the damage it can cause (Table 2).

Instituting IPM Programs in the United States

National Programs

Much of the initial impetus for developing IPM programs in the United States came from public laws that mandated roles for federal agencies or from internal policy directives within lead federal agencies. The first U.S. national IPM project was funded by the U.S. National Science Foundation (NSF), the U.S. Environmental Protection Agency (EPA), and the U.S. Department of Agriculture (USDA). The project was called the "Huffaker Project" after its coordinator, Carl Huffaker of the University of California. It ran from 1971 to 1978, catalyzing ongoing pest-control research and focusing primarily on insect pests of cotton, citrus, alfalfa, soybean, apple, and pine (Croft and Hoyt 1983). Also, beginning in 1971, the cooperative extension service of the land grant universities and the USDA initiated a number of IPM demonstration programs in alfalfa, cotton, and soybeans (Allen and Bath 1980).

The Forest Service, a branch of the USDA, began an IPM research effort in 1974 under the "USDA-Combined Forest Pest Research and Development Program." This program focused 4 to 6 years of accelerated research and development projects at federal laboratories, universities, and state schools of forestry and included work on the gypsy moth (*Lymantria dispar* L.), the Douglas-fir tussock moth, and the southern pine beetle. These collaborative efforts were phased down in 1978, 1979, and 1980, respectively. The Canada/United States Spruce Budworms Program (CANUSA) began in the minds of its leaders sometime in the early 1970s. A national symposium was held in Alexandria, Virginia, in November 1974 that brought together interested parties to start planning the program (USDA 1976). In 1978, a modest research effort began with start-up funding budgeted from the Douglas-fir tussock moth program.

U.S. federal legislation further fueled the move toward pest control on federal lands. Both the "Resources Planning Act" of 1974 (as amended by the National Forest Management Act) and the "BLM Organic Act" of 1976 called for improved management of the nation's forest resources. Forest protection of all resources and values is advocated in these mandates (Waters and Stark 1980).

Table 1
Summary of possible insect-directed techniques available for spruce-budworm/spruce-fir management (after Baskerville 1976 and Montgomery et al. 1982b)

	Use		Limitations		
Methods	strategy	Status	Research and development	Use	Potential
Chemical insecticides: larvae	3,4	6,7,8	Application efficiency	11,12	High
Chemical insecticides: adults	1,3,4	7,8,9	Application techniques Adult behavior Meteorology	12,13	Low
Chemical insecticides + disease	1,2,3,4	6,7,8,	Formulation efficiency	11,12,13	High
Bacillus thuringiensis	1,2,3,4	6,7,8	Application efficiency	12	High
Viruses	1,2,3	7,8	Virus production Application efficiency	13	Medium
Fungi	1,2,3	7,8	Spore production	13	Probably low
Microsporidia	1,2	8	Spore production	13	Low
Pheromones	1,4	7	Formulation efficiency	13	Medium
Insect growth regulators	1,2,3,4	7,8	Finding the right one	13	Medium
Host asynchrony	1,4	7,8	Finding chemical	13	Low
Native parasite enhancement	1,2	7,9	Rearing	13	Low-medium
Predator enhancement	1,2	9	Basic information	13	Low
Introduction of parasites	1,2	7,8	Finding candidates	13	Low
Genetics	1,4	8,9	Sterility techniques	13	Probably low

Codes:
1 = outbreak prevention
2 = accelerate collapse
3 = foliage preservation
4 = outbreak suppression
6 = operational
7 = field testing
8 = laboratory
9 = conceptual
11 = public sentiment and environmental aspects
12 = application efficiency
13 = undeveloped

Beginning in 1977, IPM received considerable national attention. President Carter, in his Environmental Message to Congress, identified IPM as a high priority and directed the Council on Environmental Quality, "...to recommend action which the federal government can take to encourage the development and application..." of techniques to be used in IPM (Interagency IPM Coordination Committee 1980). The Congress, in Public Law 95-113 (Section 1403, Title 14), The Food and Agriculture Act of 1977, designated the USDA as the lead agency in the federal government for the food and agricultural sciences and assigned specific missions in extension, research, and teaching. The law directed that the Secretary "...establish federal or cooperative multidisciplinary research teams on major agricultural research problems with clearly defined leadership, budget responsibility, and research programs." It further mandated that research be conducted "...to find solutions to environmental problems caused by technological changes in food and agriculture production..." and "...development and implementation through research of more efficient, less wasteful, and environmentally sound methods for producing, processing, marketing and utilizing food, fiber, waste products, other non-food agricultural products, and forest and rangeland products."

In 1978, Public Law 95-396, the Federal Pesticide Act of 1978, specifically directed the EPA to conduct IPM-related activities. Among the activities mandated were

Table 2
Summary of possible forest-directed techniques available for spruce-budworm/spruce-fir management (Montgomery et al. 1982b)

Method	Use strategy	Status	Limitations: Research and development	Limitations: Use	Potential
Salvage cutting	5	6	Application efficiency	12,14	Low-high
Presalvage cutting	1,2,4	6	Risk-rating systems Application efficiency	14	High
40-year rotation	1	6	Application efficiency	14	High
Changes in stand composition	1	6	Application efficiency cost	10,14	Medium-high
Harvest by "block cutting" in checker-board pattern	1	6	Application efficiency	14	Medium-high
Maintaining a species mix	1	6	Application efficiency Production methods cost	14	Medium
Clearcut on a 40-year rotation	1	6	Application efficiency	11,14	Medium
Developing improved road systems	1,2,3,4	6	Cost ——	14,15	Medium
Operate harvest cut following a risk-rating system	1,2,4	6	Application efficiency	13	High

Codes:
1 = outbreak prevention
2 = accelerate collapse
3 = foliage preservation during outbreak
4 = outbreak suppression
5 = salvaging timber
6 = operational
10 = inconsistant
11 = public sentiment
12 = application
13 = undeveloped
14 = institutional problems and time requirements
15 = economic costs

that the EPA administrator should coordinate IPM research with the Secretary of Agriculture. Pursuant to this mandate, a memorandum of understanding between the Secretary of Agriculture and the EPA Administrator was established in January 1979 (Allen and Bath 1980).

Later in 1979, the Office of Technology Assessment delivered a report to Congress entitled, "Pest Management Strategies in Crop Protection." Among the recommendations, the USDA was assigned responsibility and authority to coordinate IPM research programs and to implement an adequate information delivery system (Office of Technology Assessment 1979).

Within USDA'S Science and Education Administration (SEA), several reports on IPM were also produced. Among them were studies done by or for the USDA/SEA IPM Coordination Team and two of the major SEA policy committees: the Experiment Station Committee on Organization and Policy (ESCOP) and the Extension Committee on Organization and Policy (ECOP). These reports called for personnel and budgetary increases to expand IPM programs over the 1980s (Extension Committee on Organization and Policy 1979; Intersociety Consortium for Plant Protection 1979).

In 1979, a significant Council on Environmental Quality (CEQ) report, "Integrated Pest Management" (Bottrell 1979), recommended policy initiatives and additional research and education efforts to advance IPM in many disciplines, including forestry. As a consequence, President Carter, through a directive to 11 agencies, established an interagency IPM coordination committee, to modify, review, and recommend actions to promote IPM within and among agencies. This committee presented a comprehensive federal IPM interagency report to President Carter, on June 30, 1980 (Interagency IPM Coordination Committee 1980).

Twenty-two federal agencies responsible for current or potential pest control activities in six management areas (agriculture, forestry, rangeland, rights-of-way, urban environments, and public health) were identified. The total annual expenditures by these agencies for pest-control activities was estimated at $700 million with about $109 million used annually in forestry (for research, demonstration, suppression, monitoring, cooperative assistance, and so on). In addition, the report recommended a balance of efforts in assistance, implementation, research, and technology transfer.

Further, 19 recommendations were made to promote the further development of IPM programs in the various agencies.

The Reagan administration has shifted emphasis from social and environmental responsibility to military programs. Thus, many programs, including IPM, have received little or no presidential support. In fact, the Reagan administration dissolved the Council on Environmental Quality. The President's budget has not reflected explicit support for IPM, and no directives or reports have been produced. Consequently, the principal recommendation of the 1980 federal IPM interagency report — adoption of a formalized IPM policy based on a national IPM goal for federal agencies — has not been carried out. Despite this apparent lack of presidential support, agencies and individuals within these agencies, including the Forest Service, have maintained an IPM philosophy and continue to strive for development and implementation of IPM programs.

Regional Programs

IPM planning and coordination activities were established by the USDA Science and Education Administration (SEA, now the Agriculture Research Service, ARS) in 1979 for four regions — western, north-central, northeast, and southern (Allen and Bath 1980). Priorities for IPM research, extension, and teaching were established by administrative teams comprised of representatives from state agricultural experiment stations, cooperative extension services, and resident instruction. Common goals have been set for managing agricultural pests on a multistate level. Such regional planning activities have involved federal agencies, such as EPA and USDA, as well as industry, grower groups, and other interested organizations and individuals. These planning and priority setting groups are essential in regional coordination of research, extension, and teaching. Through these groups, duplication of effort is minimized and broad-based programs are developed that could not be achieved by a single state. In addition, priorities for SEA budgeting are developed and implemented.

In forestry, regional IPM programs in research and application are carried out by branches of the Forest Service. Usually, research by Forest Service scientists is coordinated at regional experiment stations. Often, research cooperative agreements are developed with states and universities within given regions.

The application of regional, IPM forest pest programs is a function of the State and Private Forestry branch of the Forest Service. Coordinated through regional field offices, regional action programs are supplemented by states within a region. Formula funding for forest pest activities is often made available to state forest management agencies for cooperative forest pest management efforts. This frequently requires matching funding by participating states.

Integrated spruce budworm programs (e.g., aerial surveys, cooperative projects, and funding) are administered by the Forest Service State and Private Forestry branch in Broomall, Pennsylvania. Coordinated through field offices in St. Paul, Minnesota, and Portsmouth, New Hampshire, cooperative federal/state spruce budworm projects have been conducted. Normally, cooperative efforts involve federal and state support apportioned about 50-percent federal and 50-percent state. Over the years, the titles of such cooperative ventures have changed to reflect a change in philosophy. For example, the 1976 program in Maine was titled, "The 1976 Spruce Budworm Suppression Project." Recently, the Maine project was called "Cooperative Spruce Budworm Integrated Pest Management Program."

State Programs

State IPM programs purposely reflect special needs and issues that are different from regional efforts. Some cooperative extension services have had agricultural IPM projects since 1972. Often these efforts are guided by statewide IPM steering committees composed of individuals from user groups and other organizations. These programs and projects usually are very successful — part of the success is attributed to the organization, structure, and mission of the cooperative extension services (Allen and Bath 1980).

Development of IPM Programs for Spruce Budworm in the Eastern United States

In the eastern United States, spruce-fir forests in several states regularly or occasionally experience spruce budworm infestations and outbreaks: Minnesota, Wisconsin, Michigan, New York, Vermont, New Hampshire, and Maine. In each of these states, a lead agency coordinates monitoring of budworm populations and damage, makes recommendations to landowners on management methodology, assists in the implementation of tactics and strategies against budworms on public and private lands, and coordinates with USDA Forest Service, State and Private Forestry, efforts in the regions. From one state to another, the relative importance of spruce-fir to the economy varies, as does the methodology for spruce budworm/spruce-fir management. To provide an appreciation of their differences, we will briefly explore ownership patterns with the hope that some comparative implications can be made.

Table 3 depicts the area of spruce-fir by state in various categories. The total area in spruce-fir implies some relative importance of the resources from one state to another. Discounting the fact that states differ in size, Maine clearly has the largest area of spruce-fir and New Hampshire contains the least. Further, the

Table 3
Area of spruce-fir by ownership (× 1 000 acres) (× 1000 ha)

	Public		Private industrial		Private nonindustrial		Total	
	Acres	Ha	Acres	Ha	Acres	Ha	Acres	Ha
Maine	330.2	133.6	4 491.2	1817.6	2 949.1	1193.5	7 770.5	3144.7
Michigan	581.4	235.3	226.2	91.5	448.5	181.5	1 256.1	508.3
Minnesota	1 408.2	569.9	150.1	60.7	384.3	155.5	1 942.6	786.1
New Hampshire	93.8	38.0	390.6	158.0	151.5	61.3	635.9	257.3
New York	97.3	39.4	157.8	63.8	469.0	189.8	724.1	293.0
Vermont	44.4	17.9	97.6	39.5	624.4	252.7	766.4	310.1
Wisconsin	317.5	128.5	86.2	34.9	337.8	136.7	741.5	300.1

total area in Maine exceeds by more than a million acres (404 700 ha) the combined total from the remaining six states.

The use and sophistication of IPM concepts and methodology depends largely on the intensity of the forest management effort directed toward the resource. Extensively managed forests used for amenities such as wildlife, recreation, and aesthetics with no management plan represents one extreme where the need for an IPM effort is minimal. At the other extreme is the intensively managed forest that is 1) closely inventoried, 2) has a management plan, and 3) has some cyclic management review process. The prime purpose of such a forest is to produce the maximum possible amount of pulpwood or sawtimber. Here the need for an IPM effort and the sophistication of the methodology is perhaps the greatest.

By exploring Table 3, we can begin to appreciate some of the forest management nuances that affect use of IPM methodology from one state to another. We have provided a breakdown of the spruce-fir acreage into "public ownership," "private industrial ownership," and "nonindustrial private ownership." To help in interpreting the implications, we generalize from these ownerships to the intensity of forest management being used on them: public-owned lands are viewed as having a multiple use objective with management plans developed and an "intensive" management in place; the private industrial ownership is regarded as one with a forest production objective, a management plan, forest monitoring, and a generally "intensive" management effort; the private nonindustrial ownership is thought of as one with an amenity value objective, no explicit management plan, and a very "extensive" form of management implied. We recognize that ownership and management intensity are not as simple as we portray, the most notable exception being the Tree Farm System, which is highly intensive management on private, nonindustrial lands. But we make our generalizations so we can begin to appreciate the differences in management intensity throughout the seven states and implications for using IPM methodology within them.

Maine has a large private industrial ownership, and New Hampshire has a large proportion of land in private industrial ownership (Table 3). This implies forest management intensity and a need for the most sophistication in IPM methodology. By contrast, Michigan, Wisconsin, and Minnesota possess large proportions of public land, with the need for IPM methodology to be varied and somewhat less sophisticated than that for Maine. New York, Vermont, and Wisconsin have a large percentage of private, nonindustrial lands. Thus, the implication is that the need for and level of sophistication of IPM methodology is somewhat lower in these areas.

To gain further information on the adoption of IPM philosophy, concepts, and methodology, we contacted representatives from each of the seven states. Table 4 summarizes our discussions with them. Each state has adopted an IPM philosophy and policy with respect to forestry in general. Maine's is the most formalized: it is spelled out in the language of state law (Rumpf et al. 1982). Wisconsin and Minnesota spell out a formal adoption of IPM in their respective state DNR management guidelines (Wisconsin DNR 1984, Minnesota DNR 1984). The remaining states have adopted an IPM philosophy and policy without an explicit written statement documenting a mandate of their objectives. We also asked each representative to detail their IPM

Table 4
Adoption of forest IPM policy/programs and specific spruce-budworm programs in states in the United States that experience spruce budworm infestations and outbreaks

State	Forest IPM-based policy-program	IPM-based spruce budworm program	Information source
Maine	Yes, formal, mandated by law	Yes, mandated by law; highly sophisticated	Tom Rumpf, Dept. Conservation, Maine Forest Service, Augusta, ME 04333
Michigan	Yes, informal multiagency cooperative	Yes, informal multiagency cooperative	Gary Simmons, Dept. Entomology, Michigan State University, E. Lansing, MI 48824-1115
Minnesota	Yes, formalized in state DNR guidelines	Yes, formalized in DNR monitoring program	Mike Albers, Minnesota DNR, Region II Headquarters, 1201 Hwy 2-East Grand Rapids, MN 55744
New Hampshire	Yes, informal	Yes, informal minimum spray policy	Stan Swier, Dept. Entomology, Nesmith Hall, University of New Hampshire, Durham, NH 03824
New York	Yes, informal	No, although some damage surveys are conducted	Mike Birmingham, Dept. Env. Conserv., 50 Wolf Road, Albany, NY 12333
Vermont	Yes, informal, multiagency cooperative	Yes, formalized multiagency program	Conrad Motyka, Dept. Forests, Parks & Rec., Div. Forestry, Heritage II, 79 River St., Montpelier, VT 05692
Wisconsin	Yes, multiagency cooperative; formalized in DNR pest management guidelines	Yes, formalized with emphasis on silviculture	Dave Hall and Allen Prey, Wisconsin DNR, Forest Pest Control, 3911 Fish Hatchery Road, Madison WI 53711

efforts specifically for spruce budworm. Again, Maine appears to have the most sophisticated program, and it is mandated by law (Rumpf et al. 1982). Minnesota, Vermont, and Wisconsin have efforts that are formalized and described (Minnesota DNR 1984; Wisconsin DNR 1984; Vermont 1983); each differs from the other in the emphasis of the methodology used. For example, Minnesota emphasizes monitoring, Wisconsin emphasizes silviculture, and Vermont has a balanced multiagency program of landowner assistance. With the exception of New York, the remaining states conduct efforts informally, with Michigan emphasizing long-term planning and prevention (Wilson et al. 1983) and New Hampshire a minimum spray policy (New Hampshire Agencies 1981). New York has no specific budworm IPM program, although some damage surveys are conducted (M. Birmingham, personal communication).

Intensity of current forest management and the need for IPM methodology varies from one locality to another in the states impacted by spruce budworm. With these differences in mind, we will now turn to the CANUSA Program and review various research and development efforts in IPM methodology to see where and how these methodologies are being used or can be used in the future.

Review of Contributions by the CANUSA Program

When we include all of the IPM methodology that provides information for decision-making and tactics for forest and insect management, the array of contributions that have resulted from the CANUSA Program is impressive. It is impossible, however, to identify every project conducted under the auspices of CANUSA or to predict their ultimate impact on IPM programs for the spruce budworm. Instead, we will highlight general areas where related developments have been made that are or could enhance an IPM approach.

Table 5
IPM methodology developed, evaluated, or adopted during the CANUSA Program by eastern U.S. investigators [1]

A. Methodology that provides information for decision-making

Methodology	Management timeframe	Developers	Evaluators	Adopters
Damage assessment	Long term/short term	Mog and Witter (1979); Witter (1981); Witter and Mog (1981); Karpinski and Witter (1982); Fowler and Witter (1982); Mog et al. (1982); Lynch et al. (1982a, b, c, d); Lynch and Witter (1983a, b, c, d); Witter and Lynch (1985); Witter et al. (1985)	Research teams measured numerous variables on permanent plots in Michigan, annually 1978-1984	Guidelines developed for Michigan land owners, private industry, and the USFS
Damage assessment	Long term/short term	Whyte (1979); Ford (1980, 1981)	Survey of spruce budworm outbreaks in Wisconsin's white spruce plantations	Recommendations made for plantation managers
Damage assessment	Long term/short term	Seegrist and Arner (1982); Solomon (1982); Schiltz et al. (1983)	Data from Maine's Growth Impact Study (Lawrence and Houseweart 1981)	Maine Forest Service and landowners
Hazard-rating system	Long term/short term	Batzer and Hastings in Minnesota (1980, 1981)	Ford (S&PF) on USFS land in Minnesota and Wisconsin (unpublished) via demonstration trials	Lake States forest owners and managers
Hazard-rating system	Long term/short term	Lynch (1984) in Michigan; Lynch et al. (1984); Witter and Lynch (1985)	Data from private industry land to validate the models	Michigan forest industries
Hazard-rating with small-format color aerial photos	Short term	Bergelin (1982); Olson et al. (1982); McCarthy et al. (1982, 1983); Olson (1983) in Michigan	Data from Michigan's ground surveys to compare and feed back at workshops in Maine, Vermont, and Michigan	Private industry in Maine
Shigometer to determine spruce budworm hazard	Long term/short term	Blanchard et al. (1983); Davis et al. (1980); Shortle (1983); Shortle and Ostrofsky (1983); Smith (1983); Smith et al. (in press)	Shigo, Davis, Shortle, and others tested the Shigometer in Maine, Vermont, and New Hampshire	Potential for use in any spruce-fir stand
Dichotomous key for choosing silvicultural treatments	Long term/short term	Flexner et al. (1983) in the Lake States	USFS on the Chequamegon National Forest via comparison with USFS silvicultural guidelines	Many in the Lake States and eastern North America

Table 5 **(continued)** [1]

A. Methodology that provides information for decision-making

Methodology	Management timeframe	Developers	Evaluators	Adopters
Site-classification of spruce-fir ecosystems in relation to spruce budworm impact	Long term	Hix et al. (1983) on Michigan's Ottawa National Forest	Model developed from German system by Barnes et al. (1982)	Private industry, USFS, and others in Michigan on small scale
Economic model for choosing treatment alternatives	Short term	Marty (1984a; 1984b) in Michigan	Presented by Marty at workshops and meetings	Maine, Michigan, and others
Pheromone trapping system	Long term/short term	Simmons (1980); Houseweart et al. (1981); Kendall et al. (1982); Ramaswamy and Cardé (1982); Ramaswamy et al. (1983)	Allen (SUNY) and many cooperators in standardized field trials	Continued trials throughout the Lake States and Northeast
Egg-mass sampling modifications	Short term	Dixon et al. (1978), a "how-to" handbook; Fowler and Simmons (1980, 1982, 1984); Montgomery (1981a, b); Waisenen (1981); Fowler and Witter (1982); Simmons and Fowler (1982, 1984); Simmons et al. (1982); Fowler (1983); Lynch (1984)	Independent data sets for validation	Michigan DNR and others
Automated egg mass counter	Short term	Carniglia et al. (1977) in Maine	Trials and further development by Jennings and Deland (1984) and others at MAG in Missoula, MT	Potential for use anywhere but mostly in Maine, Quebec, and New Brunswick
Recommendations for sampling spruce budworm on spruce	Short term	Kemp (1981) in Maine	Empirical tests	Maine and others in eastern North America
Techniques for measuring early larval dispersal	Short term	Jennings and Houseweart (1983)	Field experiments in Maine	Pest management specialists and researchers
Techniques for measuring population dynamics of parasitoids	Short term	Nyrop and Simmons (1982)	Field experiments in Michigan	Pest management specialists and researchers
Decision-making and planning model	Long term	Seymour et al. (1985) in Maine	Simultaneous trials by landowners and feedback from participants at workshops	Maine landowners

Table 5 **(continued)**[1]

A. Methodology that provides information for decision-making

Methodology	Management timeframe	Developers	Evaluators	Adopters
Spruce-fir growth and yield models	Long term	Solomon and Seegrist (1979, 1983); Solomon and Frank in Maine (1983)	Remeasurements since 1953	Maine landowners and managers
Spruce budworm woodlot management program (IPM)	Long term/short term	Rumpf et al. (1982) in Maine	Public workshops, demonstrations, seminars, news releases and corresponding trials, and public feedback	Maine woodlot owners
System for planning wood harvest and transportation	Long term/short term	Corcoran (1984); Nieuwenhuis et al. (in press); Phillips and Corcoran (in press)	Model validation techniques	Maine forest industries
Wood utilization and marketing model	Long term/short term	Govett and Sinclair (1981, 1984); Hughes and Gertjejansen (1984); Sinclair et al. (1981, 1982) in the Lake States; Bowyer et al. (1982); Barnes and Sinclair (1983); Govett et al. (1983); Sinclair and Barnes (1983); Sinclair and Govett (1983)	Research and literature reviews of the utilization and marketing of balsam fir	Northern United States when completed
IPM model for decision making	Long term/short term	Shoemaker (1981); Fleming et al. (1983, 1984); Stedinger (in press)	Model validation techniques	Maine and others in eastern North America
Needs-assessment surveys of user groups	Long term/short term	Rogan et al. (1982a, b) in the Lake States	Used to guide the Lake States Technology Transfer Program	Used by many to understand the major problems as perceived by foresters and pest management specialists
Telecommunications	Long term/short term	Rogan and Simmons (1983, 1984); Rogan et al. (1984a, b)	Formal and informal evaluations by participants	More frequent use of telecommunications in forestry
Technology transfer programs	Long term/short term	Witter et al. (1982); Frank and Okeefe (1983); Montgomery et al. (1984)	Formal and informal feedback from user groups	Numerous natural resource agencies
General information packages	Long term/short term	Montgomery et al. (1982a); Schmitt et al. (1984); CANUSA Fact Sheet and Newsletters	IPM concepts and methodology reviewed by numerous specialists	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm

Table 5 **(continued)** [1]

A. Methodology that provides information for decision-making

Methodology	Management timeframe	Developers	Evaluators	Adopters
Bibliographies	Long term/short term	Hunter et al. (1979); Jennings et al. (1979, 1981, 1982)	Lists of budworm-related publications	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm
Workshop proceedings	Long term/short term	Monitoring and evaluating spruce budworm populations; Grimble and Kucera (1984)	Summary of current techniques	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm
Workshop proceedings	Long term/short term	Utilization of balsam fir; Corcoran and Gill (1983)	Summary of current techniques	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm
Workshop proceedings	Short term	Microbials; Grimble and Lewis (1985)	Summary of current techniques	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm
Conference proceedings	Long term/short term	Forest management; Society of American Foresters (1985)	Summary of current techniques	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm
Workshop proceedings	Long term/short term	Spruce budworm impact and damage assessment; Ostaff et al. (1984)	Summary of current information	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm
Workshop proceedings	Long term/short term	Biology of host trees and the spruce budworm; Talerico and Montgomery (1983)	Summary of current information	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm
Literature review		Annotated bibliography on birds and spruce budworm by Crawford and Jennings (1982)	Summary of current information	Landowners, forest managers, students, anyone interested in spruce-fir or the spruce budworm

Table 5 **(continued)**[1]

A. Methodology that provides information for decision-making

Methodology	Management timeframe	Developers	Evaluators	Adopters
Bacillus thuringiensis	Short term	Many in agriculture and forestry	Millers (1980b); Dimond and Spies (1980); Dimond et al. (1981), and Fast and Dimond (1984) in Maine; Reardon et al. (1982), Rush et al. (1982), and Reardon and Hassig (1983) in Wisconsin; Walton and Lewis (1982) in three states; Grimble and Morris (1983), a summary; Reardon et al. (in press) in Michigan	Areas that might spray insecticides for budworm suppressions
Chemical insecticides	Short term	Many in agriculture and forestry	Montgomery et al. (1984)	Maine
Evaluating ecological impact of insecticides	Long term/short term	Bart and Hunter (1978); Hilburn and Dimond (1983)	Spray applicator field personnel	Maine
Targeted harvesting and spraying	Long term/short term	Dimond et al. (1984)	Based primarily on reassessment of previous pest management programs in Maine	Maine, although the principle can be applied to any spruce-fir forest
Techniques for monitoring environmental impact of insecticides	Short term	Adamus (1984) summarizes state-of-the-art methodology for assessing impact on aquatic ecosystems	Review by specialists	Areas that spray insecticides for spruce budworm suppression
Field test of insecticide application rates	Short term	Millers (1980a) in Maine	Operational field trials	Maine and others
NPV trials	Short term	Stairs et al. (1981)	Lab and field trials	Under development
IGR trials	Short term	Brushwein et al. (1980); Madore et al. (1983)	Lab and field trials	Under development
Develop and test new spray systems	Short term	Howitt et al. (1980); Yates and Akesson (1980a, b, c); Yates et al. (1982, 1983)	Lab and field trials	Maine and others
Strip cuts and enhancement of spruce budworm natural enemies	Long term	Standard silvicultural techniques	Trials by Nyrop et al. (1982), Michigan	Michigan, Vermont, and others

Table 5 **(concluded)**[1]

B. Tactics for treating host stands

Methodology	Management timeframe	Developers	Evaluators	Adopters
Harvesting methods to reduce wind damage	Long term	Falk (1980)	Empirical	Used in partial cuts where soils are shallow
Shelterwood, selection and clear cuts in spruce and fir stands	Long term	Standard silvicultural techniques	Trials by Frank (1983) and others to demonstrate silvicultural approaches that will minimize spruce budworm impact	Maine, Vermont, and others
Stand management of aspen-balsam fir	Long term	Standard silvicultural techniques	Batzer and Benzie (in progress) in Wisconsin to assess different cutting techniques when aspen overtops spruce-fir	Will be used by managers of mixed wood stands

[1] Many of these methodologies were developed in conjunction with projects begun or completed by Canadian researchers and other investigators throughout the world.

IPM Methodology for Use in Forest Management Decision-Making

Table 5 includes methodologies that can be used in a decision-making process, such as Simmons et al. (1984) crisis prevention and crisis response frameworks. We consider the developments of hazard-rating systems, the "Green Woods" computer model, and pheromone technology to be the most significant of the CANUSA-sponsored developments contributing to improved decision-making. Damage assessment techniques that can increase the manager's ability to estimate the current impact of the spruce budworm and hazard-rating systems to project the future effects of outbreaks on resource commodities and amenities are very useful methodologies in many areas. Models (both computer and noncomputer) that transpose these predictions into hypothetical scenarios and allow managers to project the economic and ecological repercussions of various management tactics without actually implementing them are also useful, particularly in intensive forest management. New and improved sampling methodologies help managers recognize impending outbreaks earlier than before, categorize and monitor existing outbreaks more precisely, and better evaluate management operations. As Table 5 indicates, many other contributions were made as well. More information on host stand growth and yield indicates where managers might maximize their management efforts. And a more complete picture of marketing and utilization options helps clarify the real importance of budworm outbreaks from an economic perspective.

CANUSA, aware of the importance of communication in the decision-making process, developed programs to facilitate technology transfer between and within user groups and research communities. Surveys of foresters, extension and pest management specialists, and researchers identified major management problems and various perspectives on the need and use for information. Trials with different packaging and diffusion techniques demonstrated the advantages and constraints when practitioners and researchers communicate. This led to the development of highly visible, user-oriented products such as general information packages, bibliographies, literature reviews, workshops, demonstration projects, videotapes, and various other communication techniques that improved the practitioners awareness of IPM methodologies and user willingness to try them.

IPM Methodology That Can Be Implemented As Management Tactics

To carry out the IPM decisions, management tactics such as those listed in the lower portion of Table 5 were developed or modified. We consider development of targeted harvesting and spraying and improvement in the efficacy of *Bacillus thuringiensis* to be the most significant contributions made by CANUSA on the tactics side. Improved mechanisms for applying and assessing the impact of chemical insecticides and further development and testing of alternative insect-directed treatment tactics also progressed.

Forest-directed tactics that emphasize a long-term approach, of course, require many years to implement and validate. Several silvicultural trials were conducted under the auspices of CANUSA, however, and many of the ecologically sound silvicultural tactics touted by spruce-fir managers in the early and mid-1900s are being quantified and demonstrated here in the late 1900s.

We believe that CANUSA investigators made great strides in improving the methodologies in several broad areas: acquisition and analysis of data on budworm populations and forest ecosystems, implementation and evaluation of IPM insect-directed and forest-directed tactics, and communication of the IPM approach to appropriate groups. The CANUSA Program provided a platform for developing, testing, modifying, evaluating, and disseminating new IPM methodologies. From Table 5 we see that many of the methodologies were developed for specific and diverse locations and user groups. Over the last few years, we have personally observed that the philosophy, concepts, and methodologies of IPM are being used with greater frequency, confidence, and purpose. We believe that CANUSA has helped forest managers and landowners to more fully understand their spruce budworm problems and to develop their own IPM programs to meet their individual needs and reach their management objectives.

Concluding Remarks

In this paper, we have discussed the philosophy, concepts, and methodology of IPM, particularly as they related to the spruce budworm problem in the eastern United States. The practice of IPM in forestry is directly related to the goals and needs of forest management, which we find extremely variable throughout the budworm's host range. We see that the differences in the level of sophistication of IPM programs are not only the result of economic, social political, or ecological constraints, but also are due to the status of the IPM methodologies. The philosophy and concepts of IPM in forestry are very similar for all ownerships and host types.

The philosophy of IPM is based on principles of ecology and guided by socioeconomic conditions. The IPM philosophy calls for treatment of a pest only when and where needed and in a manner that optimizes the natural mortality factors in the ecosystem. It emphasizes the need for input from a variety of specialists and de-emphasizes actions that may compound or expand the management problem.

The IPM concepts provide a framework for decision-making, interlinkage to the other components of forest management, and a guide to the implementation of IPM methodologies. The general conceptual framework changes very little from forest to forest. The major difference between frameworks is in their designated time frame. Even this difference merely changes the level of intensity of surveillance and treatment methodologies.

In general, the IPM conceptual framework begins by identifying and valuing the forest. Goals are defined and a program is established for managing individual stands. Potential pests are identified in the managed stands and their potential effect is assessed, usually according to economic criteria. Surveys are used to monitor pest populations and stand conditions. This information helps determine the need for treatment tactics.

IPM methodologies are used to implement the conceptual frameworks. These methodologies incorporate real planning or treatment tactics to solve the problem. Hazard-rating with aerial photographs over some stands, setting pheromone traps in others, and completing strip cuts in one stand in 1985 and in another in 1990 are examples of real methodologies undertaken in a spruce-fir forest. The level of sophistication of the methodologies in terms of competency determines how well we can assess a pest's status, project its impact, select the best management option, safely and effectively implement that option, and accurately monitor the consequences of our actions.

Research and development programs such as CANUSA are designed to ultimately improve methodologies. If the IPM concepts and philosophy are followed, then improved methodologies mean better IPM and better forest management programs. To decide if IPM methodologies on spruce budworm are adequate, we need to look at the present and future demands on our spruce and fir resources. We need to assess whether the sophistication of IPM methodologies is sufficient to allow forest managers and landowners to meet their goals and needs.

If managers need IPM methodologies that are more accurate, predictable, or reliable, then we believe that significant gains cannot be made until we better understand the interrelation between the pest, its hosts, predators and parasites, natural mortality factors, and how our management practices are influencing the ecosystems. IPM is based on principles of ecology. Understanding the ecosystem holds the key to producing methodologies that truly make the best use of the foundation of IPM — our concepts and philosophy.

Literature Cited

Adamus, P.R. 1984. Techniques for monitoring the environmental impact of insecticides on aquatic ecosystems. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 613. 64 p.

Allen, G.E.; Bath, J.E. 1980. The conceptual and institutional aspects of integrated pest management. BioScience 30:658-664.

Barnes, B.V.; Pregitzer, K.S.; Spies, T.A.; Spooner, V.H. 1982. Ecological forest site classification. J. For. 80:493-498.

Barnes, D.P.; Sinclair, S.A. 1983. Time related changes in specific gravity and moisture content of spruce budworm-killed balsam fir. Can. J. For. Res. 13:257-263.

Bart, J.; Hunter, L. 1978. Ecological impacts of forest insecticides: an annotated bibliography. New York Cooperative Wildlife Research Unit. Cornell University, Ithaca, N.Y. 128 p.

Baskerville, G.L., ed. 1976. Report of the task force for evaluation of budworm control alternatives. New Brunswick Dep. Nat. Res., Fredericton, N.B. 210 p.

Baskerville, G.L.; Montgomery, B.A. 1983. Spruce budworm information leaflets for the Lake States. V. Forest management. Mich. Coop. For. Pest Manage. Program, Leafl. 83-11. Univ. Mich., Ann Arbor; Mich. State Univ., East Lansing.

Batzer, H.O.; Hastings, A.R. 1980. How to rate spruce-fir vulnerability to budworm in Minnesota. U.S. Dep. Agric., For. Serv. North Cent. For. Exp. Stn., St. Paul, MN. Unnumbered leaflet.

Batzer, H.O.; Hastings, A.R. 1981. Rating spruce-fir stands for spruce budworm vulnerability in Minnesota. Pages 105-108 *in* R.L. Hedden, S.J. Barras, and J.E. Coster, tech. coords. Hazard-rating systems in forest insect pest management: symp. proc., 31 July to 1 Aug. 1980, Athens, Ga. U.S. Dep. Agric., For. Serv., Washington, D.C. Gen. Tech. Rep. WO-27.

Bergelin, L.A. 1982. Volume determination of spruce budworm damaged trees using 35 mm air photos. Master's Thesis, Univ. Michigan. 37 p.

Berryman, A.A.; Amman, G.D.; Stark, R.W.; Kibbee, D.L., eds. 1978. Theory and practice of mountain pine beetle management in lodgepole pine forests. Proceedings of Symposium, 25-27 April, 1978. Univ. Idaho, Moscow, ID.

Blanchard, R.O.; Shortle, W.C.; Davis, W. 1983. Mechanism relating cambial electrical resistance to periodic growth rate of balsam fir. Can. J. For. Res. 13:472-480.

Bottrell, D.R. 1979. Integrated pest management. Council on Environmental Quality. U.S. Gov. Printing Office, Washington, D.C.

Bowyer, J.L.; Sinclair, S.A.; Sibal, P.W.; Govett, R.L. 1982. Balsam fir — a "new" potential source of softwood lumber. For. Prod. J. 32:53-58.

Brookes, M.H.; Stark, R.W.; Campbell, R.W., eds. 1978. The Douglas-fir tussock moth: a synthesis. U.S. Dep. Agric., For. Serv. Sci. Educ. Admin., Washington, D.C Tech. Bull. 1585. 331 p.

Brushwein, J.R.; Madose, C.D.; Granett, J. 1980. Field trials with the insect growth regulator Bay Sir 8514 against the spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Maine Life Sci. Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 226. 15 p.

Carniglia, C.K.; Jennings, D.T.; Simmons, G.A.; Olson, E.T. 1977. Investigation of the fluorescence properties of balsam fir foliage for the purpose of building an automatic spruce budworm egg mass counter. U.S. Dep. Agric., For. Serv. Northeast. For. Exp. Stn. and Univ. Maine, Orono. Final Rep., Cooper. Res. Agreement 23-824. 48 p.

Corcoran, T.J. 1984. Computerized mapping and wood transportation. *In* Proceedings, Int. Union For. Res. Org. symposium on forest management planning and managerial economics 13-20 October, 1984. Univ. Tokyo, Tokyo, Japan.

Corcoran, T.J.; Gill, D.R. eds. 1983. Proceedings, Recent advances in spruce-fir utilization technology. Soc. Amer. For. Publ. 83-13. 222 p.

Coulson, R.N.; Witter, J.A. 1984. Forest entomology ecology and management. John Wiley and Sons, New York. 669 p.

Crawford, H.S.; Jennings, D.T. 1982. Relationships of birds and spruce budworms — literature review and annotated bibliography. USDA Bibl. Lit. Agric. 23. 40 p.

Croft, B.A.; Hoyt, S.C. 1983. Integrated management of insect pests of pome and stone fruit. John Wiley and Sons, New York. 454 p.

Davis, K.P. 1954. American forest management. McGraw-Hill, New York. 482 p.

Davis, W.; Shortle, W.; Shigo, A. 1980. Potential hazard rating system for fir stands infested with budworm using cambial electrical resistance. Can. J. For. Res. 10:541-544.

Dimond, J.B.; Spies, C.J., III. 1980. A comparison of Bt alone with Bt plus the additives chitinase and Orthene® in control of eastern spruce budworm. Maine Life Sci. Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 224. 14 p.

Dimond, J.B.; Spies, C.J., III; O'Neal, J. 1981. Spruce budworm: evaluation of Bt trials in Maine, 1980. Maine Life Sci. Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 237. 13 p.

Dimond, J.B.; Seymour, R.S.; Mott, D.G. 1984. Planning insecticide application and timber harvesting in a spruce budworm epidemic. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 618. 29 p.

Dixon, W.N.; Houseweart, M.W.; Jennings, D.T. 1978. How to examine branches for spruce budworm egg masses. Coop. For. Res. Unit, Sch. For. Res., Univ. Maine, Orono. Unnumbered pamphlet.

Extension Committee on Organization and Policy. 1979. Integrated pest management programs for the state cooperative extension services. USDA, SEA/CA. Ala. Coop. Ext. Service, Auburn University, Auburn, Ala. 20 p.

Falk, J. 1980. Wind damage in spruce-fir stands: a literature review with recommendations for harvesting methods. Maine Life Sci. Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 225. 25 p.

Fast, P.G.; Dimond, J.B. 1984. Susceptibility of larval instars of spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae), to *Bacillus thuringiensis*. Can. Entomol. 116:131-137.

Fleming, R.A.; Shoemaker, C.A.; Stedinger, J.R. 1983. Analysis of the regional dynamics of unsprayed spruce budworm (Lepidoptera: Tortricidae) populations. Environ. Entomol. 12:707-713.

Fleming, R.A.; Shoemaker, C.A.; Stedinger, J.R. 1984. An assessment of the impact of large scale spraying operations on the regional dynamics of spruce budworm (Lepidoptera: Tortricidae) populations. Can. Entomol. 116:663-644.

Flexner, J.L.; Bassett, J.R.; Montgomery, B.A.; Simmons, G.A.; Witter, J.A. 1983. Spruce-fir silviculture and the spruce budworm in the Lake States. Mich. Coop. For Pest Manage. Prog. Handb. 83-2. 30 p.

Flint, M.L.; van den Bosch, R. 1981. Introduction to integrated pest management. Plenum, New York. 240 p.

Ford, R.P. 1980. Spruce budworm in a white spruce plantation. U.S. Dep. Agric., For. Serv. For. Insect and Dis. Manage. Eval. Surv., Washington, D.C. NA-FB/P-5. 4 p.

Ford, R.P. 1981. Evaluation of a method to determine spruce-fir mortality caused by the spruce budworm in the Lake States. U.S. Dep. Agric., For. Serv., Washington, D.C. NA-TP. 74 p.

Fowler, G.W. 1983. The "mean of ratios" estimator for spruce budworm, *Choristoneura fumiferana* (Clem.) egg mass density. Mich. Academician 16:73-86.

Fowler, G.W.; Simmons, G.A. 1980. More accurate estimators for spruce budworm egg mass density (Lepidoptera: Tortricidae). Great Lakes Entomol. 13:151-157.

Fowler, G.W.; Simmons, G.A. 1982. Spruce budworm egg mass density on balsam fir: low to extreme population levels (Lepidoptera: Tortricidae). Great Lakes Entomol. 15:277-286.

Fowler, G.W.; Simmons, G.A. 1984. Considerations when sampling spruce budworm egg masses on balsam fir and white spruce in the Lake States: low population levels. Great Lakes Entomol. 17:97-109.

Fowler, G.W.; Witter, J.A. 1982. Accuracy and precision of insect density and impact estimates. Great Lakes Entomol. 15:103-177.

Frank, R.M. 1983. A focus on natural regeneration methods for developing a spruce fir forest less vulnerable to spruce budworm. Abstract *in* Proc. Eastern Spruce Budworm Res. Work Conf. Orono, ME. Jan. 1983.

Frank, R.; Okeefe, T.G. 1983. A transfer system to reach a selected audience: woodlot owners and mill managers. Pages 371-378 *in* B. Levi, ed. Proc., 1983 Tech. Transfer Intern. Symp.

Govett, R.L.; Sinclair, S.A. 1981. A study of the market for balsam fir dimension lumber in the Twin Cities. Timber Bull. 36:36-39.

Govett, R.L.; Sinclair, S.A. 1984. Marketing research for primary processors of northern softwood lumber. For. Prod. J. 34:13-20.

Govett, R.L.; Sinclair, S.A.; Bowyer, J.L. 1983. Lumber grade yields from spruce budworm damaged balsam fir. For. Prod. J. 33:46-50.

Grimble, D.G.; Kucera, D.R., co-chairmen. 1984. Proceedings, new and improved techniques for monitoring and evaluating spruce budworm populations. U.S. Dep. Agric., For. Serv., Northeast. For. Exp. Stn., Broomall, PA. Gen. Tech. Rep. NE-88. 71 p.

Grimble, D.G.; Lewis, F.B., tech. coords. 1985 Microbial control of spruce budworms and gypsy moths. Symp. proc., 10-12, April 1984 Windsor Locks, Conn., U.S. Dept. Agric., For. Serv., Northeast For. Exp. Stn., Broomall, PA. Gen. Tech. Rep. 100, 175 p.

Grimble, D.G.; Morris, O.N. 1983. Regional evaluation of B.t. for spruce budworm control. U.S. Dep. Agric., For. Serv., Broomall, PA. Agric. Inf. Bull. 458. 9 p.

Hilburn, H.J.; Dimond, J.B. 1983. The effects of aerial spraying for spruce budworm control with carbaryl and B.t. on non-target terrestrial arthropods. Maine Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 280. 21 p.

Hix, D.M.; Barnes, B.V.; Witter, J.A. 1983. Site classification of selected spruce-fir-dominated ecosystems for the Ottawa National Forest, Upper Peninsula of Michigan. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 83-4. 89 p.

Houseweart, M.W.; Jennings, D.T.; Sanders, C.J. 1981. Variables associated with pheromone traps for monitoring spruce budworm populations (Lepidoptera: Tortricidae). Can. Entomol. 113:527-537.

Howitt, A.J.; Retzer, H.J.; Himel, C.M.; Hogmire, H.; Ayers, G.S. 1980. Studies on the parameters which affect spray spectra characteristics from rotary sleeve nozzles. J. Econ. Entomol. 73:477-483.

Hughes, M.; Gertjejansen, R. 1984. Spruce budworm-killed balsam fir as a raw material for flakeboard and waferboard. For. Prod. J. 34:42-46.

Hunter, M.; Hacker, S.C.; Jennings, D.T.; Knight, F.B. 1979. Spruce budworms thesaurus. Maine Life Sci. Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 220. 41 p.

Interagency IPM Coordination Committee. 1980. Report of the interagency IPM coordination committee. Council on Environmental Quality, Washington, D.C., 1980 June 30. 92 p.

Intersociety Consortium for Plant Protection. 1979. Integrated pest management: a program of research for the state agricultural experiment stations and the colleges of 1890. USDA, SEA/CR, Experimental Station Committee on Organization and Policy, Washington, D.C. 190 p.

Jennings, D.T.; DeLand, L.F. 1984. Automated egg mass counter. Page 35 *in* D.G. Grimble and D.R. Kucera, co-chairmen. 1984. Proceedings, new and improved techniques for monitoring and evaluating spruce budworm populations. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-88.

Jennings, D.T.; Houseweart, M.W. 1983. Sticky-board traps for measuring dispersal of spruce budworm larvae. U.S. Dept. Agric., For. Serv., Orono, ME. Res. Pap. NE-526. 7 p.

Jennings, D.T.; Knight, F.B.; Hacker, S.C.; McKnight, M.E. 1979. Spruce budworms bibliography. Maine Life Sci. Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 213. 687 p.

Jennings, D.T.; Knight, F.B.; Hacker, S.C.; McKnight, M.E. 1981. Spruce budworms bibliography supplement 1. Maine Life Sci. Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 255. 139 p.

Jennings, D.T.; Hacker, S.C.; Knight, F.B.; McKnight, M.E. 1982. Spruce budworms bibliography supplement 2. Maine Life Sci. Agric. Exp. Stn., Univ. Maine, Orono. Misc. Rep. 268. 75 p.

Karpinski, C., Jr.; Witter, J.A. 1982. Plot size and number of plots needed to assess spruce budworm impact. Can. J. For. Res. 12:332-336.

Kemp, W.P. 1981. The significance of non-host and alternative host tree species on populations of larval spruce budworm, with emphasis on improving sampling techniques. Environ. Assoc., Inc. Orono, ME. 89 p.

Kendall, D.M.; Jennings, D.T.; Houseweart, M.W. 1982. A large-capacity pheromone trap for spruce budworm moths (Lepidoptera: Tortricidae). Can. Entomol. 114:461-463.

Lawrence, R.K.; Houseweart, M.W. 1981. Impact of the spruce budworm in the Maine spruce-fir region: 1975-1979. Univ. of Maine, CFRU, Orono, ME. Res. Bull. 3. 106 p.

Lynch, A.M. 1984. Development of sequential sampling plans for spruce budworm egg masses using Monte Carlo simulation. M.F. Thesis, Univ. Michigan. 78 p.

Lynch, A.M.; Mog. T.P.; Witter, J.A. 1982a. Impact of the spruce budworm on spruce-fir stands in the Sault Ste. Marie and St. Ignace Districts of the Hiawatha National Forest during 1978-1981. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 82-2. 24 p.

Lynch, A.M.; Mog, T.P.; Witter, J.A. 1982b. Impact of the spruce budworm on spruce-fir stands in the Munising, Rapid River, and Manistique Districts of the Hiawatha National Forest during 1978-1981. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 82-3. 28 p.

Lynch, A.M.; Mog, T.P.; Witter, J.A. 1982c. Impact of the spruce budworm on spruce-fir stands in the Bessemer, Watersmeet, Ontonagon, and Bergland Districts of the Ottawa National Forest during 1978-1981. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 82-4. 44 p.

Lynch, A.M.; Mog, T.P.; Witter, J.A. 1982d. Impact of the spruce budworm on spruce-fir stands in the Iron River and Kenton Districts of the Ottawa National Forest during 1978-1981. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 82-5. 28 p.

Lynch, A.M.; Witter, J.A. 1983a. Spruce budworm impact in 1981 on 18 spruce-fir stands in the Iron River and Kenton Districts of the Ottawa National Forest. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 83-3. 33 p.

Lynch, A.M.; Witter, J.A. 1983b. Spruce budworm impact in 1981 on 25 spruce-fir stands in the Bessemer, Watersmeet, Ontonagon, and Bergland Districts of the Ottawa National Forest. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 83-4. 49 p.

Lynch, A.M.; Witter, J.A. 1983c. Spruce budworm impact in 1981 on 17 spruce-fir stands in the Sault Ste. Marie and St. Ignace Districts of the Hiawatha National Forest. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 83-5. 33 p.

Lynch, A.M.; Witter, J.A. 1983d. Spruce budworm impact in 1981 on 21 spruce-fir stands in the Munising, Rapid River, and Manistique Districts of the Hiawatha National Forest. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 83-6. 41 p.

Lynch, A.M.; Fowler, G.W.; Witter, J.A. 1984. Development of empirical models to rate spruce-fir stands in Michigan's Upper Peninsula for hazard from the spruce budworm (Lepidoptera: Tortricidae): a case history. Great Lakes Entomol. 17:163-174.

Madore, C.D.; Boneias, D.G.; Dimond, J.B. 1983. Reduction of reproductive potential in spruce budworm (Lepidoptera: Tortricidae) by a chitin-inhibiting insect growth regulator. J. Econ. Entomol. 76:708-710.

Marty, R. 1984a. A program for evaluating the economic effectiveness of spruce budworm control with a programmable hand-held calculator. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-92. 10 p.

Marty, R. 1984b. A guide to economic evaluation of spruce budworm management opportunities in the East. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 627.

McCarthy, J.; Olson, C.E., Jr.; Witter, J.A. 1982. Evaluation of spruce-fir forests using small-format photographs. Photogramm. Eng. Remote Sensing. 48:771-778.

McCarthy, J.; Olson, C.E., Jr.; Witter, J.A. 1983. Assessing spruce budworm damage with small-format aerial photographs. Can. J. For. Res. 13:395-399.

Millers, I. 1980a. Reduced application rates of Orthene® forest spray give less effective spruce budworm control in Maine-1974. U.S. Dep. Agric., For. Serv., NA-S&PF, Broomall, PA. Rep. NA-TP-4. 10 p.

Millers, I. 1980b. Biological evaluation of aerial application of Bt against the spruce budworm in Maine — 1980. *In* Spruce budworm in Maine, the 1980 Cooperative Spruce Budworm Suppression Project. Maine For. Serv., Dept. Conserv., Augusta, Maine. U.S. Dep. Agric., For. Serv. Portsmouth, N.H.

Minnesota Department of Natural Resources. 1984. Integrated pest management guidelines. Div. For., Minn. Dep. Nat. Resour., State Hdqtrs., St. Paul. 3 p.

Mog, T.P.; Witter, J.A. 1979. Field techniques for assessing the impact of the spruce budworm (Lepidoptera: Tortricidae) in Michigan's Upper Peninsula. Great Lakes Entomol. 12:213-218.

Mog, T.P.; Lynch, A.M.; Witter, J.A. 1982. Impact of the spruce budworm (Lepidoptera: Tortricidae) on the Ottawa and Hiawatha National Forests, 1978-1980. Great Lakes Entomol. 15:1-24.

Montgomery, B.A. 1981a. An analysis of inter- and intra-tree effects on the size of spruce budworm egg masses on balsam fir. Master's Thesis, Mich. State Univ. Mich. Coop. For. Pest Manage. Prog. Inf. Rep. 81-2. 183 p.

Montgomery, B.A. 1981b. An analysis of inter- and intra-tree effects on the size of spruce budworm egg masses on balsam fir and white spruce. Master's Thesis, Mich. State Univ. Mich. Coop. For. Pest Manage. Prog. Inf. Rep. 81-3. 215 p.

Montgomery, B.A.; Simmons, G.A.; Witter, J.A.; Flexner, J.L. 1982a. The spruce budworm handbook: a management guide for spruce-fir in the Lake States. Mich. Coop. For. Pest Manage. Prog. Handb. 82-7. 35 p.

Montgomery, B.A.; Witter, J.A.; Simmons, G.A.; Rogan, R.G. 1982b. The spruce budworm manual for the Lake States — 1982. Mich. Coop. For. Pest Manage. Prog. Manual 82-6 (two printings). Sch. Nat. Res., Univ. Mich., Ann Arbor; Dep. Entomol., Mich. State Univ., East Lansing. 66 p.

Montgomery, B.A.; Dimond, J.B.; Witter, J.A.; Simmons, G.A. 1984. Insecticides for control of the spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Inf. Bull. 615. 28 p.

Montgomery, B.A.; Rogan, R.G.; Witter, J.A.; Simmons, G.A. 1984. Spruce budworm technology transfer program for the Lake States Region: a case study. Environ. Entomol. 13:1-6.

New Hampshire Agencies. 1981. Cooperative statement on major forest pest problems for 1981. Coop. Ext. Serv., New Hampshire Dep. Agric. and New Hampshire Div. For. and Lands, CES, Durham; Dep. of Agric., Durham; Dep. Res. and Econo. Dev., Div. For. and Lands, Concord. 1 p.

Nieuwenhuis, M.A.; Corcoran, T.J.; Schiltz, H.M. (In press). A map-based information system for road network management. Am. Soc. Agric. Eng. Paper NAR84-103. 6 p.

Nyrop, J.P.; Simmons, G.A. 1982. Measurements and analysis of the activity patterns of adult spruce budworm parasitoids. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 82-10. 68 p.

Nyrop, J.P.; Simmons, G.A.; Mosher, D.G. 1982. The economics of pre-salvage alternatives as a method of minimizing spruce budworm losses. Mich. Coop. For. Pest Manage. Prog. Tech. Rep. 82-9. 54 p.

Office of Technology assessment. 1979. Pest management strategies and crop protection. Vol. I. U.S. Gov. Printing Office, Washington, D.C. 132 p.

Olson, C.E., Jr. 1983. Remote sensing approaches for forestry inventory. *In* Renewable resource management: applications of remote sensing, proc. RNRF symp. on the application of remote sensing to resource management, 22-27 May 1983, Seattle, Wash. Falls Church, Va.: Am. Soc. Photo. 1983:29-41.

Olson, C.E., Jr.; Sacks, P.J.; Witter, J.A.; Bergelin, L.A. 1982. Spruce budworm damage assessment with 35 mm air photos: a training manual. Univ. Mich. Sch. Nat. Res., Remote Sensing Lab. Rep. 82-1A. 41 p.

Ostaff, D.P.; Cameron, M.D.; Mullins, E.J., eds. Proceedings of the Damage Assessment-Working Group. Workshop proc., 25-26 October 1983, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Phillips, W.; Corcoran, T. (In press). A data base system for wood harvest and transportation planning. J. Inst. Manage. Sci. (Int. Ed.)

Ramaswamy, S.B.; Cardé, R.T. 1982. Non-saturating traps and long-life attractant lures for monitoring spruce budworm males. J. Econ. Entomol. 75:126-129.

Ramaswamy, S.B.; Cardé, R.T.; Witter, J.A. 1983. Relationship between catch in pheromone-baited traps and larval density of the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. 115:1437-1443.

Reardon, R.C.; Haissig, K. 1983. Spruce budworm (Lepidoptera: Tortricidae) larval populations and field persistence of *Bacillus thuringiensis* after treatment in Wisconsin. J. Econ. Entomol. 76:1139-1143.

Reardon, R.C.; Haissig, K. 1984. Efficacy and field persistence of *Bacillus thuringiensis* after ground application to balsam fir and white spruce in Wisconsin. Can. Entomol. 116:153-158.

Reardon, R.C.; Johnson, D.; Berndt, M.; Plotta, M.; Heyd, R. (In press). B.t. applied to spruce budworms in various dosage-volume combinations in Michigan, USA. Prot. Ecol.

Reardon, R.C.; Johnson, D.R.; Narog, M.G.; Banash, S.E.; Hubbard, H.B. Jr. 1982. Efficacy of two formulations of *Bacillus thuringiensis* on populations of spruce budworm in Wisconsin. J. Econ. Entomol. 75:509-514.

Rogan, R.G.; Simmons, G.A. 1983. The feasibility of audio-cassette tapes in technology transfer: the spruce budworm technology transfer program. Mich. Coop. For. Pest Prog. Tech. Rep. 83-1. 13 p.

Rogan, R.G.; Simmons, G.A. 1984. Teleconferencing: advantages and disadvantages. J. Ext. Vol. 22:27-31.

Rogan, R.G.; Montgomery, B.A.; Simmons, G.A.; Witter, J.A. 1982a. Spruce budworm technology transfer in the Lake States: results of the needs assessment of intermediate information movers. Mich. Coop. For. Pest Prog. Tech. Rep. 82-10. 62 p.

Rogan, R.G.; Simmons, G.A.; Montgomery, B.A.; Witter, J.A. 1982b. Spruce budworm technology transfer in the Lake States: results of the needs assessment of intermediate information movers. Mich. Coop. For. Pest Prog. Tech. Rep. 82-8. 74 p.

Rogan, R.G.; Simmons, G.A.; Montgomery, B.A.; Witter, J.A. 1984a. Spruce budworm information leaflets for the Lake States. VIII. Teleconferencing. Mich. Coop. For. Pest Prog. Leafl. 84-2.

Rogan, R.G.; Simmons, G.A.; Montgomery, B.A.; Witter, J.A. 1984b. Audioconferencing: a case study from the spruce budworm technology transfer program. North. J. Appl. For. 1:52-55.

Rumpf, T.A.; Irland, L.C.; Blackmer, S.D. 1982. Spruce budworm policy in Maine: tradition, conflict and adaption. J. For. 80:708-711, 720.

Rush, P.A.; Ford, R.P.; Munson, A.S.; Croghan, C.F. 1982. Release of Dipel 4L for control of spruce budworm, Nicolet National forest, 1981: a post-suppression evaluation. U.S. Dep. Agric., For. Serv., Washington, D.C. Admin. Rep. 32-3. 7 p.

Schiltz, H.M.; Ream, G.A.; Warner, W.S.; Corcoran, T.J.; Brann, T.B.; Solomon, D.S. 1983. Impact of the spruce budworm in Maine 1975-1980. Maine Agric. Exp. Stn., Univ. Maine. Orono. Misc. Rep. 290. 35 p.

Schmitt, D.; Grimble, D.; Searcy, J., eds. 1984. Managing the spruce budworm in eastern North America. U.S. Dep. Agric., For. Serv., Washington, D.C., Agric. Handb. 620.

Seegrist, D.W.; Arner, S.L. 1982. Mortality of spruce and fir in Maine in 1976-78 due to the spruce budworm outbreak. U.S. Dep. Agric., For. Serv., Orono, ME. Res. Pap. NE-491. 3 p.

Seymour, R.S.; Mott, D.G.; Kleinschmidt, S.M.; Triandafillou, P.H.; Keane, R. 1985. The Green Woods Model — a forecasting tool for planning timber harvesting and protection of spruce-fir forests under attack by the spruce budworm. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-91.

Shoemaker, C.A. 1981. Applications of dynamic programming and other optimization methods in pest management. IEEE Trans. on Auto. Control 26(5):1125-1132.

Shortle, W.C. 1983. Effects of acute stress on fir and spruce trees vary as growth potential determined electrically. Phytopathology 73:1347. (Abstract.)

Shortle, W.C.; Ostrofsky, A. 1983. Decay susceptibility of wood in defoliated fir trees related to changing physical, chemical, and biological properties. Eur. J. For. Path. 13:1-11.

Simmons, G.A. 1980. Use of light trap data to predict outbreaks of the spruce budworm. Mich. Coop. For. Pest Manage. Prog. Inf. Rep. 80-6. 13 p.

Simmons, G.A.; Fowler, G.W. 1982. Spruce budworm egg mass density on balsam fir and white spruce: low population levels (Lepidoptera: Tortricidae). Great Lakes Entomol. 15:287-296.

Simmons, G.A.; Fowler, G.W. 1984. Considerations when sampling spruce budworm egg masses on balsam fir in the Lake States: low to extreme population levels. Great Lakes Entomol. 17:87-95.

Simmons, G.A.; Fowler, G.W.; Wilson, S.T. 1982. How to apply bias adjustment to spruce budworm egg mass counts. Mich. Coop. For. Pest Manage. Prog. Inf. Rep. 82-11. 11 p.

Simmons, G.A.; Cuff, W.; Montgomery, B.A.; Hardman, J.M. 1984. Integrated pest management. *In* D. Schmitt and J. Searcy, eds. Managing the spruce budworm in eastern North America. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb., No. 620.

Sinclair, S.A.; Barnes, D.P. 1983. Toughness of healthy and spruce budworm-killed balsam fir. For. Prod. J. 33:24-26.

Sinclair, S.A.; Govett, R.L. 1983. Production and distribution of balsam fir lumber in eastern North America. For. Chron. 59:128-131.

Sinclair, S.A.; Govett, S.B.; Bowyer, J. 1981. Potential lumber grade yields from balsam fir and spruce budworm-killed balsam fir. Timber Prod. Bull. Apr. May: 10-11.

Sinclair, S.A.; Barnes, D.P.; Govett, R.L. 1982. A preview of balsam fir utilization research. North. Logger Timber Process. 30:16-17, 28.

Smith, K.T. 1983. Indexing fir and spruce trees for decay susceptibility. Phytopathology 73:837. (Abstract.)

Smith, K.T., Blanchard, R.O.; Shortle, W.C. (In press). Cambial electrical resistance related to the number of vascular cambial cells in balsam fir. Can. J. For. Res.

Society of American Foresters (Region VI). 1985. Spruce-fir management and spruce budworm. Proc. Tech. Conf., 24-26 April 1984, Burlington, Vt.; U.S. Dep. Agric., For. Serv.. Broomall, PA. Soc. Am. For. 84-07. Gen. Tech. Rep. NE-99. 217 p.

Solomon, D.S. 1982. Spruce budworm impact on the spruce-fir forest in Maine: An integration of spatial information systems. Pages 1046-1050 *in* Proc., Soc. Am. For. In-place resource inventory workshop, 9-14 August 1981. Orono, ME.

Solomon, D.S.; Frank, R.M. 1983. Growth response of managed unevenaged northern conifer stands. U.S. Dep. Agric., For. Serv., Orono, ME. Res. Pap. NE-517. 17 p.

Solomon, D.S.; Seegrist, D.W. 1979. Growth and yield analysis of thinned and even-aged spruce and fir stands in Maine. *In* Proc. Int. Union For. Res. Org. Working Group S4, 01-02, Vienna, Austria.

Solomon, D.S.; Seegrist, D.W. 1983. Growth and yield analysis of thinned and even-aged spruce and fir stands in Maine. Pages 149-156 *in* Planning, performance, and evaluation of growth and yield studies. 1979 September, Int. Union For. Res. Org. Subject Group S4.01, Oxford, England; Commonw. For. Inst., Oxford Univ. Press, Occas. Pap. 20.

Stairs, G.R.; Fraser, T.; Fraser, M. 1981. Changes in growth and virulence of a nuclear polyhedrosis virus from *Choristoneura fumiferana* after passage in *Trichoplusia ni* and *Galleria mellonella*. J. Invert. Path. 38:230-235.

Stedinger, J.R. 1984. A spruce budworm-forest model and implications for suppression programs. For. Sci. 30(3) 597-615.

Talerico, R.L., Montgomery, M., tech. coords. 1983. Proceedings, forest defoliator — host interactions: a comparison between gypsy moth and spruce budworms. 5-7, April, New Haven, Conn. U.S. Dep. Agric., For. Serv., Broomall, PA. Gen. Tech. Rep. NE-85. 141 p.

Thatcher, R.C.; Searcy, J.L.; Coster, J.E.; Hertel, G.D., eds. 1980. The southern pine beetle. U.S. Dep. Agric., For. Serv. Sci. Educ. Admin. Washington, D.C. Tech. Bull. 1631. 267 p.

USDA. 1976. Proceedings of a symposium on the spruce budworm. U.S. Dep. Agric., For. Serv., Washington, D.C. Misc. Publ. No. 1327. 188 p.

Vermont Department of Forestry, Parks and Recreation. 1983. Spruce budworm problem analysis. Agency Environ. Conserv., Dep. For., Parks and Rec., Div. For., Montpelier, Vt. 18 p.

Waisanen, L. 1981. Applying the negative binomial distribution to spruce budworm egg mass sampling for damage prediction in balsam fir stands in the Upper Peninsula of Michigan. Master's Thesis, Univ. Michigan. 51 p.

Walton, G.S.; Lewis, F.B. 1982. Spruce budworm core Bt test — 1980, combined summary. U.S. Dep. Agric. For. Serv., Orono, ME. Res. Pap. NE-506. 12 p.

Waters, W.E. 1974. Systems approach to managing pine bark beetles. *In* T.L. Payne, R.N. Coulson, and R.C. Thatcher, eds. Southern pine beetle symposium. Proceedings of Symposium, Texas Agric. Exp. Stn., College Station.

Waters, W.E.; Stark, R.W. 1980. Forest pest management: concept and reality. Ann. Rev. Entomol. 25:479-509.

Whyte, G.L. 1979. Spruce budworm damage in spruce plantations on the Nicolet Forest-1978. U.S. Dep. Agric., For. Serv., Broomall, PA. S&PF Eval. Rep. NA-FR-11. 7 p.

Wilson, L.F.; Mosher, D.G.; Simmons, G.A. 1983. Michigan's cooperative forest pest management program, a team approach to improving forest management. Great Lakes Entomol. 16:109-114.

Wisconsin Department of Natural Resources. 1984. Fir/spruce pest management guidelines. Wisconsin Dep. Nat. Resour., For. Pest Manage.

Witter, J.A. 1981. Techniques for assessing the impact of the spruce budworm in Michigan. Pages 529-540 *in* 17th World Congress Proc., Int. Union For. Res. Org., Vol. 2.

Witter, J.A.; Mog, T.P.; 1981. An integrated approach for assessing spruce budworm damage, and developing a hazard-rating system and stand models for spruce-fir stands in Michigan's Upper Peninsula. Pages 45-51 *in* R.L. Hedden, S.J. Barras, and J.E. Coster, tech. coords. Hazard-rating systems in forest insect pest management: symposium proceedings. U.S. Dep. Agric. For. Serv., Washington, D.C. Gen. Tech. Rep. WO-27.

Witter, J.A.; Lynch, A.M. 1985. Rating spruce-fir stands for spruce budworm damage in Eastern North America. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. 636.

Witter, J.A.; Simmons, G.A.; Montgomery, B.A.; Rogan, R.G. 1982. Technology transfer in forest pest management: a case history. Great Lakes Entomol. 15:297-302.

Integration of Forest Management and Pest Management in the Eastern Provinces of Canada

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The role of Integrated Pest Management Systems (IPMS's) is discussed in relation to forest management planning in the eastern provinces of Canada, viz., Ontario, Quebec, New Brunswick, Nova Scotia, Newfoundland, and Prince Edward Island. CANUSA did not succeed in producing and implementing an IPMS for eastern Canada. The reasons for this are examined. Land ownership and management objectives and practices vary greatly within the eastern provinces. These differences and misconceptions about the nature of decision-making in forest management made the development of an IPMS suitable for the variety of forest management agencies throughout eastern Canada impossible within the time available. Suggestions are put forward about how spruce budworm researchers might better be able to help forest management.

Le rôle des systèmes de lutte intégrée est discuté en rapport avec la planification de l'aménagement forestier dans les provinces de l'Est: Ontario, Québec, Nouveau-Brunswick, Nouvelle-Écosse, Terre-Neuve, Île-du-Prince-Édouard. Le programme CANUSA n'a pas réussi à faire élaborer et exécuter un système de lutte intégrée pour l'est du Canada. Les raisons en sont examinées. Les formes de propriété foncière et les méthodes et les objectifs de l'aménagement varient beaucoup dans les provinces de l'Est. Ces différences et les fausses conceptions sur la nature de la prise de décisions en aménagement forestier ont rendu impossible, dans les délais accordés, l'élaboration d'un système de lutte intégrée qui conviendrait à la gamme des organismes d'aménagement forestier de cette région. Des solutions sont proposées pour aider les chercheurs qui étudient la tordeuse des bourgeons de l'épinette à mieux aider les aménagistes.

Introduction

Integrated Pest Management is a philosophy that evolved in agriculture within the past 25 years in response to problems created by an over-reliance on chemical control. In the early days the idea went under the name of Integrated Control and simply advocated an integration of biological and chemical methods to achieve more effective control. Pest populations were determined at which the pests caused significant damage, i.e., the Economic Injury Level, and control was applied only when needed to keep the pest population below this injurious economic level. The name Pest Management emerged from Integrated Control as an attempt to put greater emphasis on the resource. Later socio-economic factors were added and the "integrated" idea from Integrated Control was brought back into an important position; the expression Integrated Pest Management (IPM) was invented to reflect this movement.

Predecessors of the Canada/U.S. Spruce Budworm Program, viz., the U.S. Douglas-fir tussock moth and U.S. mountain pine beetle studies, adopted the IPM philosophy to pest management, and especially took a systems approach (Ruesink 1976) to their work (Waters and Stark 1980). So-called Integrated Pest Management Systems (IPMS's), or comprehensive mathematical models, were developed as decision-support tools (Franz 1976). The CANUSA Program intended to develop an IPMS for the spruce budworm and then use it to "provide resource managers with guidelines for rational decisionmaking" (sic) (McKnight and Buckner 1981, p. 4).

Was this objective attained for the eastern provinces of Canada? (We have tried to minimize use of the expression "eastern Canada" because its meaning varies across the country.) The answer is unambiguous: no. The reasons why not are less simple. In this paper we analyze the nature of decision-making, especially as it relates to the contribution of decision-aiding models. We also provide extensive detail on forest and pest management practices in the eastern provinces. Finally, the organizational structure of CANUSA — along with its evolution is described in detail, concentrating on those impediments that inhibited the production of an IPMS for the eastern provinces. We note that CANUSA failed to account for the multiple rational and intuitive ways by which forest management decisions are made. CANUSA also failed to account in its research planning for the diversity of forest management practices in eastern Canada, making it difficult to see how an IPMS would have been used even if it had been produced. To conclude the study, we put forward suggestions that we think could lead to better research support of forest management clients.

Pest Management is a Component of Forest Management

Although both pest management and forest management are common expressions, it should not be forgotten that pest management is a component of forest management. Pest management as it relates to forest pests is really protection of the forest ecosystem to allow forest managers to control, or regulate, the amount or timing of the availability of various benefits from the forest. In this definition (Baskerville 1983, unpublished MS; Baskerville and Montgomery 1983) benefits are taken to include nonindustrial as well as industrial goods and services including wood products, wildlife, recreational opportunities, and so on.

In a related definition of forest management, Ford-Robertson (1971, pp. 107-8) refers to it as "the practical application of scientific, economic and social principles to the administration and working of [an area, whatever its ownership, used for forestry purposes] for specified objectives."

Baskerville (1983, unpublished manuscript) and Baskerville and Montgomery (1983) see forest management in terms of four tasks: scheduling of the harvest or other use, distribution of the products of the harvest or use, renewal of the resources and, as mentioned above, protection of the resource. This last task is, of course, the prime objective of pest management practices.

How Are Decisions Made?

A corollary of the systems approach to pest management is a rational approach to decision-making: "with the forest management systems approach now being developed, it should be evident that a method of decision analysis is needed that is biologically rational and adaptable to the information outputs from the predictive models in the system" (Waters and Stark 1980, pp. 499-500). A rational "integrated multidisciplinary research and development effort" is envisaged as providing "essential backup" (Waters and Stark 1980) for the forest manager to do his job of choosing between the options — benefits and costs — provided by the comprehensive model. (See the IPMS of Fig. 3 in Waters and Stark 1980). To get some idea as to whether alternative models of decision-making can limit the rational, scientific model advocated by the systems approach to IPM, it might be useful to look briefly into the decision-making literature.

Operations Research (OR) has been defined as the science of decision-making (Gass 1983, p. 603), in terms of developing and applying decision-aiding models. This definition restates succinctly an earlier 1975 definition by Lonnstedt (quoted by Mintzberg 1980, p. 128): "Operationally defined, operations research (OR) consists of a class of mathematical/statistical research techniques which have come to be utilized for solving problems likely to arise within organization." To these authors at that time the emphasis in OR was clearly on the model.

From 1950 to 1970, OR successfully applied mathematical models to "operational decision problems" (Gass 1983, p. 604), notably routine ones concerned with planning and control (Mintzberg 1980, p. 101). Beginning in the late 1960s, OR-based methodology began to be applied to policy-level decisions. This was a logical development as improvements of managerial decisions which aim at implementation of existing policies can be useless — or even counter-productive — when the policies themselves are in need of reformulation (Mintzberg 1980). But the extension of the methodology to the policy level of organization did not meet with the same success as the OR methodology had at the operational level, and a search for the limiting factors began.

The search is now about 15 years old, during which time the various approaches to decision-making have come under considerable discussion. The assumption that the best (if not the only) form of decision-making is data based, comprehensive, and rational has been strained. In OR literature this view, called the "rational comprehensive" approach to organizational decision-making (Giesen and Radford 1983), was exclusive until the late 1950s. This approach assumes that it is possible to list all available alternatives, determine the associated outcomes and preferences over these outcomes, and choose the rational alternative leading to the most preferred outcome.

This comprehensive approach was challenged in the early 1960s by one referred to as "incrementalism" (Braybrooke and Lindblom 1963, as cited in Giesen and Radford, 1983). In this approach the decision maker considers only alternatives that differ marginally from the status quo; he assumes that negative consequences can be remedied by further marginal adjustments. He is not confident of his ability to list all available alternatives and finds it impossible to separate these completely from his goals.

Recently, the rational comprehensive approach has been said to suffer from a hyper-rationality trap (Roberts 1980) and the incremental approach from a subrationality trap (Giesen and Radford 1983); these traps clearly stem from one's perception of the adequacy of available knowledge. When knowledge is considered to be complete, one is presented with the option to look globally at the problem and rationally choose the best option: the hyper-rationality trap occurs if a poor decision is made because of excessive reliance on incomplete information, or attempted quantification of intangibles. When one is concerned that available knowledge may be inadequate for the task at hand, and also that decisions based on the knowledge available may lead in undesirable directions from which further changes in direction may be difficult, the tendency is to forego dramatic changes from the status quo — even if desirable — and tinker: the subrationality trap occurs if reliable data are ignored because of excessive conservatism. Scientists concerned with decision-aiding models tend to fall into the hyper-rationality trap, by inclination and by precedent of scientific history.

The hyper-rationality trap emerged for OR practitioners as they turned their attention to policy problems which almost by definition are difficult to formulate (i.e. "squishy"; Gass 1983, p. 604) and for which needed reliable data are often not available. According to Mintzberg (1980) there are five oft-mentioned problems limiting successful implementation of models developed to support policy-level decisions: 1) managers resist analysis because they don't understand it (or the people who do it); 2) managers resist a scientific approach to problem solving because they haven't been sold on it; 3) solutions based on scientific analysis are resisted because they lack the support or participation of top management; 4) resistance to scientific analysis can be explained by managerial attitude and organizational climate; and 5) politics in the organization block or distract the use of scientific analysis. Mintzberg (1980, p. 107) suggests that all of these explanations do help to limit implementation but suggests that the problem is deeper yet: "Communication and selling can be done effectively, support and participation can be evoked, hospitable attitudes and climates can be found, politics can be circumvented (or used), and yet policy analysis can and often does still fail."

Mintzberg (1980) believes that scientific, or rational, analysis yields one — and only one — perspective, and not one obviously superior to others. Some limitations of rational analysis include the following:

1. A model-based analysis tends to assume policy making to be the orderly sequential process reflected in the construction and form of models; yet managers make many of their decisions quickly, to seize a fleeting opportunity or to respond to an unforeseen crisis.
2. Scientific analysis tends to avoid areas for which appropriate data are not available; managers tend to rely on "soft" data — data that are not (yet) factual, not quantified, and often nonquantifiable. (Of course, models can, and often do, incorporate guesswork but the guesses of people who are not experienced in the abstraction of soft data: Mintzberg (1980) states that managers spend 60 to 80 percent of their time in verbal communication.)
3. Some people suggest that scientific analysis is objective and not reflective of any particular value system; Mintzberg (1980) disagrees with this suggestion, arguing that the need for analysis of certain "data" (e.g., an objective function) puts a value on certain types of information that can be justified on the basis of analytical expediency alone. Also, the choice of model type can influence the decisions based on it; it is not difficult to choose a model type and/or data to get desirable results. It seems, then, that scientific procedures are not value free and objective.
4. Because scientific analysis often takes time and simplifies the process modeled, it tends to be used most successfully in highly centralized (for model simplicity) and bureaucratized (for ready implementation) organizations.
5. The assumption is made that scientific analysis is suited to the needs of policy making; in fact, policy making tends to be characterized by fluxes, calling for groping, interactive processes with emphasis on trying to grasp the big picture.

In short, Mintzberg (1980) sees policy makers routinely dependent upon intuition, based upon past experiences, and upon discussion. In his view scientific analysis will succeed as scientists recognize the weaknesses of intuition and supplement it by analytical thinking; one might also add that scientific analysis will succeed as scientists recognize the strengths of intuition and add to them. Mintzberg (1980) discusses this approach but gives no pat answers as to how to do this. Indeed, it seems axiomatic that pat answers, or routine methodological approaches, will not work. What is suggested is the application of a variety of sciences to decision-making: open-ended problem exploration.

Mintzberg (1980, p. 129) calls his approach "soft analysis." It "maintains a division of labour between manager and analyst, but one concerned more with time than cognitive style. The manager is busy, plugged in; the analyst ... has time to probe deeply into issues. Soft analysis mutes the differences in cognitive style, calling on the analyst to inject a dose of intuition into his otherwise analytic approach ... Analysis becomes "a continuing dialogue rather than a one-shop service" .. linking up with intuition without sacrificing its basic distinctiveness. As Ornstein [1972] ... notes 'Our highest creative achievements are the products of the complementary functioning of the two modes. Our intuitive knowledge is never explicit, never precise in the scientific sense. It is only when the intellect can begin to process the intuitive leaps, to explain and "translate" the intuition into operational and functional knowledge that scientific understanding becomes complete'... Above all, soft analysis calls for ... people comfortable with numbers but not obsessed with them, capable analytical types who also have intuitive skills and are not shy to use them, people ... who can open up issues instead of closing them prematurely" (Mintzberg 1980, p. 129, 130).

We have taken Mintzberg's (1980) paper to represent the state of belief regarding problems with implementation because it makes sense to us, not because it necessarily represents the widely-accepted view. He makes the basic point that scientists and managers represent different cognitive styles, each with its own limitations: "The [intuitive] people tend to act before they think, if they ever think; and the [analytic] people think before they act, if they ever act" (p. 122). He suggests that scientists should complement the intuition of the manager and puts forward four suggestions as to where analysis can help policy makers: the scientist can give another perspective to the policy maker, one the manager is inclined to overlook; he can help in diagnosing the policy problems; in political situations, conflicting scientific experts can expose errors in thinking, reveal important assumptions, and generally raise the level of debate; and the scientist can, if intimate with the policy-making situation, conduct useful "real-time" analysis for the manager under pressure.

Now, with this background in mind, let us look briefly at the situation with IPM decision-aiding models. Much work in the past decade has involved building comprehensive, or all-inclusive, simulation models with the expectation — but not the reality — of implementation. The approach has been very strongly in the genre of rational comprehensive. From the industrial-user side has come some skepticism, pointing out the IPM's are of no merit unless they "fit corporate needs in arriving at administrative and management decisions" (Connor 1976, p. 227). IPMS developers have not, in our opinion, adequately considered the interests and constraints of the model users; too often the user is simply something like: "a forest manager who is charged with making decisions."

From those model makers who have tried to implement existing work has come the view (Bakus 1982, p. 502) that more "well-trained and skillful decision analysts" are needed (Mintzberg's first of the oft-mentioned views regarding implementation failure), and the view (Whalon and Croft 1984, p. 464) that "IPM implementers ... will need to enlist sociologists to gain a better understanding of the innovation-adoption process" (Mintzberg's fourth point).

One recent paper (Mumford and Norton 1984, p. 172) has come closer to Mintzberg's (1980) conclusion in suggesting that "an appreciation of the behavioral characteristics of farmers' decision making in regard to pest control is crucial if appropriate pest management practices are to be developed and implemented." This brief description of the state-of-the-art in the systems approach to IPM suggests that we can profitably learn from the experience of OR practitioners.

Wherever an IPMS is expected (explicitly or implicitly) to solve all problems for all clients, it will probably be too general to compete with other methods at an operational level and will suffer from the hyper-rationality trap at policy and planning levels. As a general rule, it would seem desirable that those building decision-aiding models know as much as is practicable of their client's problems, interests, and constraints. OR experiences suggest that only with this background can one map out a research program that has a reasonable chance of being used.

Forest Management in the Eastern Provinces of Canada

This section reviews the effects of the spruce budworm from the viewpoint of landowners in the eastern provinces of Canada. The detail that follows is included because it illustrates the complexities that an organization like CANUSA must take into account in its planning and in the implementation of its plan if it is to support forest management practice in eastern Canada. This section sets the standard against which the success of the CANUSA organization will be judged. However, once having obtained a feel for the nature and diversity of approaches, some readers may prefer to skip onto the next section. This may be done without sacrificing an understanding of the major conclusions of this paper.

Table 1
Some basic statistics on forested land in the eastern provinces of Canada

Provinces	Total forested land[1] (1000km^2)	Productive forested land[2] (1000 km^2)	Soft/Mixedwood land[3] (%)	Fir volume[4] (million m^3)	Spruce volume[4] (million m^3)
Newfoundland	142	79	92/7	47	46
Nova Scotia	42	28	49/32	38	76
Prince Edward Island	3	N/A	37/35	8	13
New Brunswick	65	59	38/48	118	154
Quebec	624	489	66/20	978	1780
Ontario	432	331	51/32	157	1292
Total	1308	986	—	1346	3361

[1] Table P4, Bonnor (1982).
[2] Table P7, Bonnor (1982): stocked, productive, non-reserved forested land.
[3] Map No. 6, Bonnor (1982): percent of stocked, productive (reserved and non-reserved) forested land.
[4] Table P14, Bonnor (1982): gross merchantable on stocked, productive, non-reserved forested land.

Land Area and Ownership

Table 1 presents some basic statistics on forested land in the eastern provinces of Canada. The major inventories exist in Quebec and Ontario; this ranking applies to all variables listed (except percent mixedwood) and Quebec is notably ahead in fir volume, having 6 times that of Ontario. However, in Quebec the softwood stands form a band above the mixedwood type (Map 6, Bonnor 1982) and easily accessible areas of both Quebec and Ontario are covered by mixedwood forests. In fact, only Newfoundland is covered by a fairly uniform blanket of softwood forest; elsewhere in eastern Canada accessible and productive mixedwood forests (25-75 percent coniferous) are the norm.

Table 2 provides some information on ownership of land in eastern Canada. In terms of total holdings, the provincial Crown is the dominant owner of forested land. Federal holdings are insignificant except, perhaps, in Ontario. Private land tends to be located mainly in the more accessible and warmer regions. For example, all forested land in Quebec south of the St. Lawrence River (but not in the Gaspé region) and almost all of Nova Scotia is privately held (Map 3, Bonnor 1982). Much of the land in New Brunswick adjacent to the U.S. border and the Bay of Fundy is privately held.

Forest Management Objectives

Some organizations set out formal objectives which, if implemented, can simplify descriptions of the behavior of the organization. Furthermore, the use of objectives is regularly recommended by the various branches of pest management, operations research, and the scientific community generally.

It is noteworthy, then, that we were unable to find stated objectives by provincial government departments in charge of managing Crown lands. However, objectives are specified in the federal-provincial Economic and Regional Development Agreements (ERDA) and in the associated Subsidiary Agreements. For example, the 1984 Canada-New Brunswick Forest Renewal Subsidiary Agreement (Canadian Forestry Service, 1984a) states:

"2.2 (a) Pursuant to Section 3 of the ERDA, the general objective of this Agreement is to provide a means for direct federal financial support to initiatives in the intensive management of New Brunswick's forests to combat an impending timber shortage and to ensure continuing employment opportunities.

(b) More specifically, pursuant to the objective stated in Subsection 2.2(a), the major objectives of this Agreement are:

Table 2
Area (1000 km²) of forested land in various provinces in eastern Canada, subdivided by ownership. From Table P3 in Bonner (1982)

Province	Ownership Classes				
	Federal	Provincial	Private	Other	Total
Newfoundland	1.51	134.90	5.98	0.01[1]	142.40
Nova Scotia	1.18	10.88	29.43	0.00	41.49
Prince Edward Island	0.00	0.00	0.00	2.94[2]	2.94
New Brunswick	1.58	30.54	32.40	0.00	64.52
Quebec	1.85	555.81	66.34	0.00	624.00
Ontario	6.94	381.46	43.44	0.07[2]	431.91
Total	13.06	1113.59	177.59	3.02	1307.26

[1] Owned by municipalities.
[2] Undetermined.

(i) To immediately encourage and support forest management for the purpose of endeavouring to increase the present sustainable supply of softwoods to an average 7.2 million cubic meters (m^3) annually, from the forest resource to help ensure the continued viability and competitiveness of the present wood-based industry.

(ii) To conduct projects and studies to expand on the knowledge base for forest management planning and development thus more effectively and efficiently realizing the goals of intensive forest management programs.

(iii) To upgrade private woodlot management through technical and financial assistance for woodlot development activities other than those directly related to increasing the softwood supply of timber; and, to increase income and employment opportunities in the production of quality specialty products."

About private holdings, we could find some stated objectives. For example, in their 1983 Annual Report, Abitibi-Price write that it

> "is an integrated forest products company that also manufactures groundwood papers, fine papers, kraft pulp, building products and lumber. In addition, the company has a nationwide paper converting and distributing operations and is, through partnerships, involved in mining and exploration activities.
>
> Our fundamental goal in all of these operations is to achieve the highest possible standards in safety, product quality, customer service, earnings, return on investment and development of our human resources. This goal is reflected in our dedication to communication as the key to trust and credibility, to employee participation and involvement as a leadership style, and to cooperation in employee relationships."

The dominant concerns of Abitibi-Price are thus: human safety, product quality, customer service, earnings, return on investment, and "human resource" development. Presumably they would welcome aid in terms of decision-support techniques in any of these areas. (Note that the company has not listed continuity of wood supply as a dominant concern.)

Abitibi-Price developed and implemented a strategic plan a few years ago (1983 Annual Report). Strategic plans, like IPM's, try to view the long-term from insight provided by comprehensive models. Yet one should not assume that strategic plans are in commonplace use in corporations, as Millar's (1984) article begins with the observation that although more than 90 percent of the U.S. Fortune 1000 companies claim to do some type of strategic planning, there is dissatisfaction among business leaders with mobilizing their organizations to move toward the execution of their stategic plans. We did not try to determine what percentage of the forest companies in eastern Canada state explicit company objectives.

Turning from corporate private landowners (large freehold), we now consider the individual private landowners (woodlot or small freehold). Reports available for Ontario (Smyth and Nausedas 1982) and New Brunswick (New Brunswick Private Woodlot Resources Study 1983) suggest that objectives, although defined, vary among the woodlot owners and among regions of each province.

Ontario (Table 13, Smyth and Nausedas 1982) found objectives which included part of the property, multiple reasons, affinity for woodland, fuelwood, recreation, selling timber, benefit to farm operation, etc. Northern Ontario owners cited cutting fuelwood as a main reason more often than did owners in Southern Ontario.

For Ontario as a whole, about 44 percent of all landowners having woodland on their properties stated that their main reason for retaining it was that woodland had always been a part of the property. Less than 1 percent maintained woodland primarily as a result of local legal requirements. About 55 percent of all landowners specified one or more of the other objectives listed above for owning woodland.

The New Brunswick study (New Brunswick Private Woodlot Resources Study 1983, p. 44) divided the owners into primary sector workers (19 percent), blue-collar workers (22 percent), white-collar workers (22 percent), and pensioners and housekeepers (26 percent), and found these groups viewed their objectives rather differently. Objectives included: part of a farm holding, a second home, a permanent residence, firewood production, financial investment, affinity for woodlot, selling timber, recreation, and Christmas tree/maple sugar production. No figure is directly available in the study report for the proportion of woodlot owners specifying objectives, although about 37 percent of all owners of forested land listed "part of a farm holding" as one of three primary reasons for owning forested land. Also, about 38 percent of all owners did not plan to undertake any management activities in the future.

Federal government holdings are managed through the Canadian Forestry Service. It has a formal objective: to maintain and enhance the flow of economic, social, and environmental benefits from Canada's forest resource for the long-term benefit of Canadians (Canadian Forestry Service, 1984b). In a 1974 report (Canadian Forestry Service) a similar activity objective was broken down into 7 subactivities, each with their subactivity objective. Subactivities included: 1) forest policy and program planning; 2) production forestry research, development, and application; 3) environmental and amenity forestry research, development and application; 4) background research; 5) operations; 6) extension services; and 7) international forestry.

Under subactivity 2 there was a component called "Damage control," with the objective "To discover, develop, improve and demonstrate practical means of predicting, preventing, detecting and controlling large scale destruction of forests and trees." Under subactivity 5 there was a component called "Forest insect and disease survey," with the objective "To monitor the occurrence and impact of forest and tree insects and diseases, to assess their implication for forest management and to disseminate the findings to appropriate agencies." Although many of these objectives still apply, the program activity structure has since been changed and separate objectives have not been assigned at the subactivity (SA2) level.

Thus the federal government is in the business of researching and developing pest management systems. The role of other landowners is unclear with respect to pest management.

Forest Management Practices

Where it is not possible to get to know an organization by its stated objectives, it is always possible to infer such information by studying its practices. We do this now by major classes of landowners (provincial Crown, corporate private, and individual private) and by province. The treatment is, of course, selective and, given our reliance on readily accessible publications, will be out of date in places.

Quebec

In the last two decades the province of Quebec has made considerable efforts to rationalize its forest-based industry (Lortie 1984). Reed and Associates (1978, p. 50) cautioned against using old statistics: "Major changes are bound to occur in forest management, which will be considerably increased."

The resultant forest management plan is ambitious, depending heavily on extensive data collection and processing, including modeling (Lussier 1976). Crown land is subdivided into 44 management units and, in some cases, subdivided again; all units are managed on a sustained-yield basis. Long-term allocation and management plans are prepared on provincial and management unit levels.

A formal algorithm is used to define the provincial allocation and management plan (Lussier 1976). Based on the definition of sustained-yield units, a sophisiticated simulation model is used to calculate allowable cut (or wood supply estimates) incorporating various management and utilization alternatives. Uses other than wood production are considered at this point. A wood demand analysis by consuming centers, e.g., a mill, is then conducted. Various modes of transportation and distances from origins to destinations are determined and a wood cost matrix, including harvesting, transportation, and management costs, is constructed.

A linear programming model uses wood supply by sustained-yield unit, wood demand by destination, and cost by origin and destination, i.e., the cost matrix, to determine a theoretical optimum allocation. Then, considering the actual allocation, this solution is adjusted using a simulation model to obtain more realistic results. The model, MODAS (Le Modèle d'Allocation et de Simulation), is run a "sufficient number of times to arrive at an acceptable allocation for a given set of management and utilization hypotheses" (Lussier 1976, p. 46).

This allocation process is applied to a set of management and utilization hypotheses and the resulting set of allocation plans are evaluated by a socioeconomic model. The alternatives are evaluated in terms of criteria such as discounted cash flow at the provincial level, cost/benefit analysis, number of jobs created, and wood cost.

In this way the most desirable allocation and management plan for the whole province is obtained. Preliminary management and utilization objectives for the various management units are also retained from this analysis, and serve as a starting point for the preparation of plans at the management unit level.

Planning at the management unit level includes two parts: a long-term resource development and utilization plan; and precise resource allocation to the various users toward preparing their renewable wood supply contracts. The long-term plan is prepared by the algorithm used for the provincial plan, with the aim of establishing more precisely the objectives retained from the provincial plan. For this purpose three documents are prepared.

The so-called biophysical document provides the information needed to make an analysis of allowable cut in relation to management, wood harvesting, and utilization alternatives. An allowable cut simulation model is used to examine a large number of alternatives and simulate in time and space the progress of wood harvesting operations. Many operational constraints are retained in the analysis. Silvicultural and logging costs constitute a part of the output. The subdivision of the management unit into small utilization units constitutes the basis of allowable cut calculations and wood allocation to various users.

The socioeconomic document includes the wood demand analysis and the demand for uses other than wood production. It also provides information on infrastructures, and a labor supply and demand analysis.

The synthesis document is the result of an analysis of supply and demand, with the aim of getting more precise management and utilization objectives than established in the provincial study. If the final objectives are quite different from the preliminary ones, the provincial study will be adjusted accordingly until there is a perfect correspondence between the overall provincial plan and plans prepared at the management unit level.

The final two steps consist of allocating wood supply areas to the users and preparing the short-term management plan. This plan is based on a more intensive forest inventory than used above and it indicates precise actions that must be taken immediately to reach the retained objectives, along with cost and personnel estimates. Organizational structures responsible for the execution of the various activities constitute an important part of the plan. The manager is given some control tools to readjust the plan whenever major deviations from predicted performance occur.

The whole management plan operation can be subdivided into five phases: 1) preparation of decisions, 2) decision-making, 3) plan of activities, 4) execution and control, and 5) plan revision. Phases 1 and 3 have been sketched above. Phase 2, decision-making, is to be made as the Quebec Ministère de l'Energie et des Ressources and other Departments choose from the management alternatives provided by the model. Wood-user collaboration with the plan is also essential.

A version of the MFRC/UBC budworm model called OSCAR (Outil de Simulation de *Choristoneura fumiferana* pour l'Aménagement des Résineux) (Hardy 1978; Jones 1979) is also used in Quebec province although its use has not yet been integrated into the forest management system.

In its implementation phase, this forest management plan has apparently run into difficulties (Lortie 1984). Reed and Associates' (1978) caution may once again be relevant: "Major changes are bound to occur in forest management."

Private pulp, paper, and other companies harvest the timber on the Crown lands under 20-year wood procurement contracts on well-defined geographical areas (Reed and Associates 1978). The purpose of this Crown forest (forêts dominiales) type of wood allocation was to move the Quebec government from a policing function to a planning and managerial role.

The Quebec government also runs extensive forestry assistance and incentive programs for private forestry in the province. These programs are the most comprehensive in Canada (Ontario Ministry of Natural Resources 1982).

Insecticide spraying has taken place in Quebec province from as long ago as 1954 (Irving and Webb 1981), managed by the government with the actual spraying done under contract by private companies. Protection against spruce budworm is the single most important item of the provincial forestry budget (Reed and Associates 1978). The objective of the spray program is a combination of tree protection and maximum budworm kill (Irving and Webb 1981).

The current outbreak was discovered in 1967 in western Quebec (Paré 1983) and by the peak year when 35 million ha (86.5 million acres) were infested, 2.6 million ha (6.4 million acres) were sprayed (Canadian Forestry Service 1979). The outbreak is located in the southern part of the province, around the St. Lawrence River. The Quebec government began a spraying program in 1970, until 1976 mainly in Southwestern Quebec and thereafter in the Gaspé, where 0.81 million ha (2 million acres) were sprayed in 1978 (Canadian Forestry Service 1979). This document also notes that the decision to restrict control activities to the Gaspé was based on the assumption that the loss of balsam fir and white spruce north of the St. Lawrence could be compensated for by the increasing availability of black spruce and jack pine chips from more northerly regions as byproducts of the sawlog industry. Since shipping these chips to mills in the Gaspé was considered impractical, the balsam fir protection was continued there (Canadian Forestry Service 1979). Spraying generally begins after one year of severe attack and continues until the infestation is substantially reduced (Paré 1983).

Private holdings account for only 11 percent of forested land (Table 2), and only 17 percent of the private land is in holdings larger than 810 ha (200 acres) (Ontario Ministry of Natural Resources 1982). Thus small owners account for most of the freehold, although not of the freehold cut (Reed and Associates 1978).

Private land in Quebec province is largely centered in the extreme south of the province, along the St. Lawrence River (See Figure 1 of Belzile 1981). There are 125,000 landowners (40 percent farmers) with an average of 50 ha (124 acres) of forested land. Four million m^3 (17 billion board ft) of softwood are harvested annually, 25 percent of the wood supplied to industry. This 25 percent, one might note, is grown on 11 percent of Quebec's forested land. A private forest inventory program was begun in 1980, to be completed in 5 years. The program is expected to provide an essential tool for implementing forest development activities (Belzile 1981), a step forward in developing the potential of private forests.

Ontario

In 1962 a new policy saw full responsibility for regeneration and stand management given to the provincial Department of Natural Resources, leaving private industry responsible only for harvesting. This led to problems (Reed and Associates 1978) and a 1979 amendment to the Crown Timber Act resulted in forest companies assuming forest management responsibilities (Armson et al. 1980).

Management in Ontario takes the form of Management Plans, Operating Plans, Ground Rules, and Annual Plans for every forest management agreement negotiated between the Ontario government and a forest company. Plans are prepared by the company in consultation with staff of the Ministry of Natural Resources.

The Management Plan aims to provide for continuity of management in a 20-year period, related to a management objective of sustaining the wood supply for a mill or mills to meet market requirements. The Management Plan is seen as a first step in developing shorter-term plans. Components of the Plan include description of the area, provisional annual allowable cut (AAC) estimate, capacity to supply mill requirements, surplus estimate, anticipated change in forest structure, subdivision of the forested area, accessibility, administrative procedures, and implementation details (Armson et al. 1980).

The Operating Plan covers a 5- to 10-year period (van Fraassen 1983) providing a location of the operating area, land base revisions, (short-term) objectives, access, final AAC estimate, allocation of the AAC, a forecast of silvicultural activities, summary of activities for the past 5 years, and administrative procedures (Armson et al. 1980).

The Ground Rules provide the guidelines including silvicultural specifications, standards, and other information that will apply to the agreement area for a 5- to 10-year term concurrent with the operating plan.

The Annual Plan states the actions that will be carried out during the year to put the Operating Plan into effect. Components include access, proposed cutting area, proposed silvicultural activities, extended forecast of silvicultural activities, and administrative procedures (Armson et al. 1980).

In this management scheme, the model OWOSFOP, the Ontario WOod Supply and FOrest Production model, is used for wood supply forecasting (for details on use, see Armson et al. 1980). (OWOSFOP is a derivative of New Brunswick's WOSFOP, WOod Supply and FOrest Productivity model [Hall 1978]).

The Ontario government runs the following programs to assist private forest landowners: Provision of Planting Stock Program, Woodlands Improvement Program, Advisory Services Program (Forestry Extension), Managed Forest Tax Reduction Program, and Agreement Forests Program (Ontario Ministry of Natural Resources 1982).

Budworm does not seem to be of widespread concern in Ontario. Van Fraassen (1983, p. 60) points out that the forest management planning system just described does "not contain much information in regard to the spruce budworm infestation and its control." He notes that forest area depletion is 70 percent harvest cut and only 6 percent burns plus blowdown and all insects and diseases, and suggests that the spruce budworm must produce a proportionally larger depletion effect before it obtains a proportionally larger consideration in management planning. One might argue that both loss of growth potential and depletion by death as effects of spruce budworm should have been considered — nevertheless, van Fraassen's (1983) paper does reflect one perception of the effects of the spruce budworm in Ontario. The Canadian Forestry Service (1979) points out that current cutting practices and fire protection are favoring the establishment of balsam fir. Hence they expect much of the productive forested area will show an increase in balsam fir in the next rotation.

Carrow (1983) adds to van Fraassen's (1983) discussion by describing Ontario's 1979 Policy and Procedure for Budworm Spraying. Spray programs are authorized for epicenter suppression, outbreak containment, and protection of high-value or commercially-operable forests. High-value forests currently sprayed include investment protection (e.g., seed orchards), aesthetic value (e.g., provincial parks), and ecological value (e.g., fish or wildlife habitat) categories. Commercially-operable forests are also sprayed but with selection criteria that ensure only short-term protection (maximum of 3 years) with directed or accelerated harvest being complete within 5 years of the start of spraying.

Private holdings account for only 10 percent of forested land (Table 2), but they account for a disproportionately larger amount of industrial wood (Ontario Ministry of Natural Resources 1982). Five companies own 9 720 km^2 (3,752 mi.^{2}), or 52 percent of all private forested land in northern Ontario. Algoma Central Railway owns 3 443 km^2 (1,329 mi.^{2}) of forested land. Since 1978 the Railway has managed its land for production of wood and timber, for protection of the natural environment in the public interest, and for a long-term program of tourist and recreational development. Abitibi-Price Inc. owns 2 618 km^2 (1,010 mi.^{2}) and its primary objectives for this land are to triple the yield of wood fiber on their productive forest lands, and to locate and develop mineral resources as economically feasible. Domtar Inc. owns 1 675 km^2 (646 mi.^{2}) in northern and eastern Ontario; its main objective is wood production, with secondary objectives including recreation and hunting. Newaygo Timber Company Ltd. owns 1 451 km^2 (560 mi.^{2}) in northern Ontario. Spruce Falls Power and Paper Company Ltd. owns 765 km^2 (295 mi.^{2}) of forest land with an objective to maximize the yield of wood fibers. Further detail is available in Ontario Ministry of Natural Resources (1982).

Coniferous forest types account for only 15 percent of the total land area owned privately; given the location of the land of the five corporate owners just discussed, we may infer that individual private landowners are not important contributors of industrial softwood in Ontario. Indeed, a census of such landowners (Ontario Ministry of Natural Resources 1982) found only 3 percent of them interested in selling timber. Of those owners who carried out forest management activities on their properties, only 6 percent did so to provide wood for sale. There are 154,000 individual private landowners (45 percent farmers) with some woodland on properties of 20 ha (50 acres) or more.

Newfoundland

Newfoundland contains 142 000 km^2 (54,812 mi.^{2}) of forested land, but only 56 percent is stocked, productive land (Table 1). The forest is predominantly softwood (Table 1), essentially balsam fir and black spruce (Canadian Forestry Service 1979) and owned by the province (Table 2), although the distribution of ownership is not even. The Crown exercises control over all forested land in Labrador (3.6 million ha [8.9 million acres] plus 1.9 million ha [4.7 million acres] not inventoried in detail, or 5.5 million ha [13.6 million acres] estimated), with cutting rights on most of this land held by a Crown corporation, Labrador Linerboard Ltd. (Reed and Associates 1978). On the Island of Newfoundland the tenure picture is more complicated due to the mixture of old long-term tenures and freehold rights which came into effect before any accurate forest inventory data were generally available. Reed and Associates' (1978) Table 40 gives the distribution of tenure on the Island as: Crown unalienated 13 950 km^2 (5,385 mi.^{2}), Crown lease and license 18 610 km^2 (7,184 mi.^{2}), private freehold 4 980 km^2 (1,922 mi.^{2}), and other 350 km^2 (135 mi.^{2}).

Two private companies (Bowater Newfoundland Ltd. and Abitibi-Price Inc.) hold rights to 60 percent of the Island's productive forest (Reed and Associates 1978). About 90 percent of private freehold is held by these companies, as is about 98 percent of Crown lease and license. The latter is held under 99-year leases which do not begin to expire until after the year 2000.

A 1974 Forest Land (Management and Taxation) Act allowed the Newfoundland Forest Service to assume the initiative and responsibility for forest management in the province (Reed and Associates 1978). The province is divided into 19 Forest Management Units, including one for Labrador. Management is carried out by the companies under regulations prescribed by the province. Companies are requested to prepare 5-year management plans covering all of their forested lands (irrespective of the form of tenure) and submit them to the Forest Service. They are also required to report annual harvests in terms of area and volume in accordance with the Forest Management Unit system. The government levies two levels of taxation: a higher one for unmanaged forest land.

The province had an appreciable volume of overmature timber susceptible to insect and disease attack (Reed and Associates 1978) but the recent budworm outbreak has reduced this volume. The long-range strategy is to improve road access for age class adjustment by harvesting overmature stands. The short-term strategy is chemical control by aerial spraying (Reed and Associates 1978).

The spruce budworm is a major forest pest problem; 90 percent of the productive forested area of the Island was infested in 1977 (Munro et al. 1979). Forest protection in Newfoundland is the responsibility of the Forest Service. They undertook sizeable spraying operations in 1977-78 but have since deferred to public opposition (Irving and Webb 1981).

Individual private landowners hold only about 11 000 ha (27,181 acres) (Ontario Ministry of Natural Resources 1982). There are no specific private land forestry programs in the province.

New Brunswick

Although New Brunswick has a relatively small forest base, about 91 percent of its land is productive (Table 1).

The province owns only 47 percent of the forested land (Reed and Associates 1978), substantially lower than any of the provinces discussed so far. By 1974 virtually all Crown forests were licensed to private companies, in most cases to augment private sources of supply (Reed and Associates 1978).

Forest management in New Brunswick was passed onto licensed companies by the implementation of the Crown Lands and Forest Act in 1982. The basis of tenure on a Crown Timber License is a Forest Management Agreement negotiated between the Department of Natural Resources and the licensee. Licensees must prepare Industrial, Management, and Operating Plans covering all activities of the licensee and any sub-licensees. The Industrial Plan covers a period of 25 years and describes all aspects of the licensee's wood processing facility, including plant investment, employment levels, plan and production capacity, end product production levels, all expected sources of wood for the facility, markets to be served, and other information as required by regulation. This Plan must be updated every 5 years.

The Management Plan also covers a period of 25 years. It is intended that the Plan shall describe the objectives for the Crown Land used by the licensee and sub-licensees (but sustainable harvest is assumed); describe the manner in which the licensee will manage the Crown lands with respect to silviculture, timber harvesting, forest protection, road construction and maintenance, forest recreation, fish and wildlife, watershed protection, general land management, and other matters prescribed by regulation; and provide other information as required by regulation. The Plan must be updated every 5 years.

The Operating Plan covers a period of 5 years. It is intended that the Plan shall identify the proportions of wood supply to be used in any wood processing facility of the licensee or any sub-licensee; and describe the operations the licensee and sub-licensees will carry out, with information on integration of operations, including the areas in which harvesting is to be carried out, the quantity to be harvested, the conditions under which harvesting will be carried out, the sharing of harvest responsibilities, management and costs, silvicultural treatments, the distribution of wood harvested, and other information required by regulation. The Operating Plan must be consistent with the Management Plan and is evaluated and updated annually. More detail on this Plan may be found in the New Brunswick Forest Management Manual (New Brunswick Department of Natural Resources 1978).

In this management scheme, the model WOSFOP, the WOod Supply and FOrest Productivity model (Hall 1978) is used for wood supply forecasting.

The Department of Natural Resources sets the management standards and then, every 5 years, audits reports of performance relative to set standards in all forest resource management activities on the License. To a substantial extent, this audit will determine the Department's recommendation on renewal of the Forest Management Agreement.

Since 1976 the New Brunswick Department of Natural Resources has administered a private land forestry program. It provides support for management of private lands up to 4 000 ha (9,884 acres) in size, where the owner is not involved in pulp and paper manufacturing (Ontario Ministry of Natural Resources 1982). Projects under the program include the Woodlot Owner Educational and Information Project, the Technical Services and Assistance Project, and the Public Information Services Project (New Brunswick Private Woodlot Resources Study, 1983).

In 1978 Reed and Associates noted that the spruce budworm is the "overwhelming problem in forest management facing the provincial government in New Brunswick." This report also noted that the New Brunswick Crop Protection Program has cost $95 million (1976 dollars) since it began in 1952, but has allowed industry to increase the annual harvest from about 4 million m^3 to 7 million m^3 (17 billion board ft to 29.6 billion board ft).

Spraying was planned and conducted from the beginning by a nonprofit corporation, Forest Protection Ltd. Initially, shares were held by four pulp and paper companies and the New Brunswick government, with the latter holding the controlling shares. Cost-sharing was set at approximately one-third industry, two-thirds government, and for a number of years the federal government contributed half the government share. Over the years the number of industrial sponsors has increased to nine (Irving and Webb 1981). Recently the responsibility for planning the control operation passed to New Brunswick's Department of Natural Resources (Webb and Irving 1983). Forest Protection Ltd. still retains operational responsibilities.

The objective of the spray program remains as it was developed: tree protection from budworm attacks by limiting the amount of defoliation (Irving and Webb 1981; Baskerville 1983). Largely because of past spruce budworm outbreaks the forest age structure is such that there is deficiency of stands in the 20-40 year old age classes (Canadian Forestry Service 1979), suggesting an impending wood shortage.

Private holdings account for 50 percent of forested land (Table 2); about 18 percent (LeBlanc 1981) to 23 percent (Ontario Ministry of Natural Resources 1982) is held by corporate private landowners. About 40 percent of these lands are held by J.D. Irving Ltd., and about 25 percent by Fraser Inc. (Maritimes Forest Research Centre, unpublished report). J.D. Irving Ltd. is noted for intensive management of many of its forest holdings.

Some forest companies provide assistance to woodlot owners (Ontario Ministry of Natural Resources 1982; New Brunswick Private Woodlot Resources Study 1983). Assistance has taken the form of forest management and planning advice, demonstration woodlots, subsidized seedlings, subsidized silviculture, and an instance of equipment donation for establishment of a computerized forest management system.

Individual private landowners number 35,000 in New Brunswick and account for around 29 percent (Ontario Ministry of Natural Resources 1982) to 34 percent (LeBlanc 1981) of the forested land. The importance of woodlots has increased with the policy incorporated in the Crown Lands and Forests Act that private forested lands shall be the primary source of timber for wood processing facilities in the province. Since 1977 Forest Protection Ltd. has had to avoid spraying near year-round habitations, hence many private woodlots have not been protected (Webb and Irving 1983). According to LeBlanc (1981, p. 12), protection for private woodlots is now being discussed, but he says woodlot owners "will accept to be informed, educated, encouraged to do one thing rather than another, ... etc., but they will not be forced, either by legislation or by corporation pressures, to relinquish their freedom of choice." However, LeBlanc (1981) has noted that only 1 percent of individual private woodlands in New Brunswick experience some sort of management activity.

Nova Scotia

Nova Scotia contains 28 000 km^2 (10,808 mi.^{2}) of productive forested land (Table 1). Of this, 71 percent (Table 2) is held privately, and over two-thirds of this land (52 percent of total forested land in the province) is held in small parcels of less than 400 ha (988 acres) (Reed and Associates 1978). According to Reed and Associates (1978, p. 53) such "fragmentation of private ownership poses serious problems for future forest management, and is one reason why the government seeks to increase Crown holdings up to one-third of the forest land in Nova Scotia."

Slightly more than one-half of provincial Crown land is leased to the forest industry or is under a stumpage agreement. The licensee is responsible for preparing a harvesting plan (Reed and Associates 1978). Nova Scotia Forest Industries holds the license for all licensed Crown land in Cape Breton Island and for the majority of licensed land on the mainland (Maritimes Forest Research Centre, unpublished report); the company has no private holdings in Nova Scotia. An intensive forest management program was begun in 1971 but a lapse in forest protection made this effort less meaningful than it might have been.

The management agreement of 1971 between Nova Scotia Forest Industries and the Department of Lands and Forests did not explicitly allow for protection of licensed lands from budworm attack: the budworm was not considered a major threat to the forests of eastern Nova Scotia (Baskerville and Weetman 1978). So, on the basis of a concern for public health (Baskerville and Weetman 1978, p. 1-23), the Nova Scotia government denied requests in 1976 and 1977 by the company to protect threatened forest land. No protection was afforded to the forests of Cape Breton Island during the outbreak of the 1970s and 1980s (Baskerville 1983) and losses did occur (Ostaff 1982; Baskerville 1983). Losses of 78 percent of the growing stock on the Cape Breton Highlands occurred by the end of 1981; for both the Highlands and Lowlands regions, the combined mortality of fir and white spruce to 1981 was 53 percent of the growing stock. Final mortality will be higher yet. In wood supply terms, the effect of this mortality means less than one-third of the softwood AAC will be available without budworm damage beyond the current decade (Baskerville 1983).

During the past two decades forest production from small woodlots in Nova Scotia has dropped from 68 percent of total provincial harvest to 32 percent (38 percent of pulpwood) as cited in Johnson (1981). This author also reported that the total harvest was exceeding the AAC by about 15 percent in softwood.

The financial losses implicit in these statistics are dramatic, especially for a province where the forest industry is the most important resource-based industry, amounting to about $600 million annually (Johnson 1981). Decisions to increase the productivity of the forests were made and implemented in the late 1970s, funded 80 percent by the federal government and 20 percent by the Nova Scotia government (Ontario Ministry of Natural Resources 1982). Various assistance plans have been devised requiring forest management plans, and there is no shortage of applications from woodlot owners, but "the prospects of intensive forest management being practiced on the majority of small woodlots are not very bright" (Johnson 1981, p. 2). Reed and Associates (1978) echoed that concern: "it is now a problem of finding the money to fund the program" (Johnson 1981, p. 5).

Corporate private landowners number four (Johnson 1981), but only Scott Maritimes Ltd. and Bowater Mersey Paper Co. Ltd. hold large freeholds (Maritimes Forest Research Centre, unpublished report). Three of the larger companies participated in a provincial private land forest management program, and in 1980 carried out various silvicultural treatments on 13 000 ha (32,123 acres) of their 727 000 ha (1.8 million acres) holdings; less than 1.8 percent of their land (Johnson 1981).

Scott Maritimes Ltd. offers a Woodlot Management Program to woodlot owners. The company agrees to manage the landowner's property and pay a fair market value for the forest products the company harvests (Ontario Ministry of Natural Resources 1982).

Prince Edward Island

Prince Edward Island contains under 3 000 km^2 (1,158 mi.^{2}) of forest land (Table 1), of which about 2 500 km^2 (965 mi.^{2}) is productive forest land (Reed and Associates 1978). According to Reed and Associates (1978) and the Ontario Ministry of Natural Resources (1982), 90 percent of the land is privately owned; Table 2 classifies all Prince Edward Island land as undetermined.

Less than 100 years ago, Prince Edward Island had a forest-based industry that included shipbuilding, export of timber, and sawmilling. Uncontrolled harvesting has reduced the resource to a condition where even commercial exploitation of pulpwood is a marginal proposition. Fifty percent of the indigenous forest has now been destroyed (Reed and Associates 1978).

Protection against insects is left largely to the private landowners.

"The future of the forests in Prince Edward Island rests largely with the private sector and their attitude toward reforestation. ... A favorable combination of accessibility, moderate climate and excellent site quality provide the necessary physical conditions for an expanded silvicultural program" (Reed and Associated 1978, p. 56).

Do Objectives and Practices Match?

As stated above, objectives are fashionable. Suffice it to cite Economic Injury Level for IPM; objective functions in optimization models so popular in Operations Research; strategic planning starting off with the objective of the organization and devising a plan to reach this objective.

A major class of landowner, provincial Crown, either does not use management objectives for the overall use of their land, or if objectives do exist, does not publish them. Their practice, with respect to forestry uses of their land, at least, is different. There we see that objectives are specified for specific tasks, e.g., federal-provincial forestry agreements. Also provincial-company agreements specify objectives: Quebec manages its land on a sustained-yield basis; Ontario aims to provide continuity of management in a 20-year period, by sustaining the wood supply to individual mills to meet market requirements; New Brunswick lets the individual license holders define objectives on their license, on a 25-year base, which the New Brunswick government accepts or rejects. New Brunswick is unique in demanding that licensees, under the Forest Management Agreements, manage their license for a variety of uses including fish and wildlife and forest recreation. Provinces not mentioned do not have — or have not bothered to publish — objectives for forest management programs.

We did not search private corporate literature sufficiently to see how many corporate landowners prepare objectives for their companies, and hence their land. But Millar's (1984) article does note that more than 90 percent of the U.S. Fortune 1000 companies claim to do some sort of strategic planning — and hence it does not seem far fetched to assume that many corporate landowners in eastern Canada do have company objectives along the lines published by Abitibi-Price for its freehold in northern Ontario. These objectives of Abitibi-Price (triple the yield of wood fiber on productive forest lands; develop mineral resources as economically feasible) are not inconsistent with company objectives.

Among individual private landowners, we found documented evidence of a number of defined objectives, or rather an array of them.

It is noteworthy that the federal government with very little land in eastern Canada (Table 2) has the most elaborate set of objectives. Many of these relate to helping other agencies on their land and hence achieve national objectives. Perhaps the conflict between the obvious national interest of forested land throughout Canada and the virtual lack of federal Crown lands has necessitated a clear statement of the role of the federal government (Winget 1984).

It seems from this comparison that, where defined, objectives and practice are complementary — suggesting that objectives have useful roles to play. But objectives are defined for various purposes, presumably as it seems useful, rather than as a necessary correlate of land ownership. Objectives, defined outside those that can be inferred as implications from action/practice, do not seem essential to running an organization.

Inferred objectives were apparent, at times, from a description of the current state of forestry practice. For example, the New Brunswick Forest Management Manual shows that the Minister responsible for passing the Crown Lands and Forests Act wanted to put forest management on a business-like basis: according to the Manual, the management system applies a principle of accountability analogous to that in a public company (New Brunswick Department of Natural Resources 1982). The shareholders collectively own the company and engage a management team to run the company operations. The management team has full management responsibility and authority but they are regularly and systematically accountable to the owners. The manner and style of that accountability is defined by the owners, who require an audit of the performance of accounts before acceptance.

In this case, the owners of the Crown land are the people of New Brunswick, and the provincial government, through their Department of Natural Resources, acts on their behalf. The Licensee provides the management team and reports to the Department as prescribed in the Forest Management Manual (New Brunswick Department of Natural Resources 1982). An Advisory Board is set out under the Act to advise the Minister on matters related to the management of Crown land; the settlement of disputes with respect to the management of Crown land; and other matters submitted by the Minister (New Brunswick Crown Lands and Forests Act, Section 69[1]).

Research Support of Forest Management

Integration of forest management and pest management will occur as pest management practices relate to the needs and practices of forest management systems. It is very clear from the previous section that forest management systems are rather diverse in eastern Canada. Thus it is useful to ask if there was appropriate diversity in pest management research and development conducted under the CANUSA umbrella to allow the results of that research to take their rightful role within forest management in the eastern provinces of Canada? Put in other words: did the planning of pest management research in CANUSA take into account the diversity of forest management approaches in eastern Canada, and respond so that the research results would be usable by forest managers throughout the east? In answering this question, we will look at research in eastern Canada that came under the CANUSA banner.

CANUSA: Objectives and Practices

The principal basis for CANUSA was a plan for a R&D program in the U.S.A. prepared in late 1974 and early 1975 (Runyon et al. 1983). CANUSA began with a Memorandum of Understanding between the Department of Environment of Canada and the United States Department of Agriculture, signed in 1977. In December 1977, a meeting was held in the western United States to develop a plan for CANUSA; it modified the United States plan of 1974-75. A related meeting was held in Montreal in January 1978 to provide a perspective for an eastern Canada-U.S. component. Another meeting followed closely to review plans developed at the previous two meetings. A composite plan was prepared from which an "Activity Schedule" for a joint program evolved.

According to the Memorandum of Understanding the primary objective of CANUSA was:

> "to design and evaluate management strategies for control of the spruce budworms and/or management of budworm-susceptible forests which will assist forest managers to attain management objectives in an economically and environmentally acceptable manner."

Sub-objectives are also listed in this document:

> "— Develop and improve methods for assessing and predicting budworm population levels and forest responses to budworm attacks;
> "— Improve existing control technology and develop environmentally acceptable chemical, biological, and silvicultural treatment techniques;
> "— Develop and improve methods for assessing and predicting short- and long-term impacts of budworms on forest resource uses and values;
> "— Develop strategies for integrating pest and resource management systems; and
> "— Monitor and evaluate each management strategy (system) to assure that it is environmentally acceptable."

The Activity Schedule was intended to be a master plan which would allow investigators to see how their work fitted into CANUSA's objectives and sub-objectives, and which also could be used by CANUSA management to select study proposals and to inform them about progress. It was "the framework for coordination of all research and development on spruce budworms related to Program objectives and identifies opportunities for cooperation between all program investigators and components" (McKnight and Buckner 1981, p. 1).

This 1981 document provides incredible detail on all CANUSA work from 1979 through 1983, including "Projected Outputs" from the various studies at the end of CANUSA in 1984. The Activity Schedule was said to be a "dynamic document ... reviewed and revised annually by Program Management as part of the annual planning and budgeting process" (McKnight and Buckner 1981, p. 1).

Under a section titled Program Structure and Approach, CANUSA was said to consist of "Activities" organized by a smaller set of "Targets" and "Subtargets." Targets approximate the Sub-objectives as stated in the Memorandum: Sub-objective 1 (minus "assessing ... budworm population levels") is similar to Targets 1 and 2; Sub-objective 2 is similar to Target 4; Sub-objective 3 is similar to Target 3; Sub-objective 4 is similar to Target 6 (except that the Sub-objective talks about strategy development whereas Target 6 talks about providing "budworm management information" (McKnight and Buckner, 1981, p. 4); Sub-objective 5 is equivalent to Target 5.

The major conceptual change that occurred during the evolution from the 1977 Memorandum Sub-objectives to the 1979 Activity Schedule Targets is that by 1978, information was said to develop within Activities and flow "from one target to another, ultimately converging in Target 6 to provide resource managers a variety of action alternatives and guidelines, i.e., integrated pest management systems for spruce budworms" (McKnight and Buckner 1981, p. 2). Thus we see that the systems approach to IPM was in place by 1979 at least. Following this philosophy a neat, systematic approach to research planning was envisaged: "At the outset of the Program, and throughout its duration, available information is assembled and evaluated to identify gaps in knowledge and research and development needs" (McKnight and Buckner 1981, p. 2).

Target 6 is quoted from the Activity Schedule because, as quoted above, the IPMS is the final product for "resource managers":

> "*Target 6 — Pest/resource management systems.* — Resource managers must consider management action alternatives against the spruce budworms in both economic and environmental terms. Economic evaluation is provided by integrating information on budworm populations (Target 1), stand dynamics (Target 2), and economic impact (Target 3) to predict the economic consequences of uncontrolled budworm infestations. Information on the effectiveness and costs of various treatment strategies (Target 4) will allow resource managers to evaluate the likely benefits and costs of proposed treatments in the context of the pest situation, stand projections, and resource economics. Added knowledge of potential environmental impacts of various management strategies, including no action, will provide resource managers with guidelines for rational decisionmaking [*sic*]. Special emphasis will be placed on delivery of budworm management information to resource managers in forms most useful to them."

Activities were tasks "to be completed by conducting one or more studies or projects in the duration of the Program" (McKnight and Buckner 1981, p. 2). The activities by year and political subdivision (eastern Canada, western Canada; similar U.S. designations) can be very detailed; for example Target 1, Subtarget 1.1, Activity 1.1.1 for an eastern U.S. study, year 1979 starts: "Relate light trap catches to defoliation. Pheromone trap design." Investigators were not assigned to the various studies listed under each Activity even though political subdivisions were designated.

In March 1978 the Joint Planning Unit (four members from Canada appointed by the Director General of the Canadian Forestry Service) reviewed the Activity Schedule, and the Canadian members proposed a task force review of "on-going eastern programs ... with a view to establishing work priorities and interfacing and coordinating, not only the on-going program, but also the accelerated components, both Canadian and U.S." (Runyon et al. 1983, p. 9). Apparently by the time the task force was organized it included Americans (Runyon et al. 1983) but applied only to eastern Canada, and in fact only to research done by the Canadian Forestry Service. Its name defines its limitations well: Task Force for the Review of CFS Research on the Eastern Spruce Budworm. Its terms of reference makes reference to CANUSA (p. A5) but only insofar that in the 5 years of overlap between the Task Force's program and CANUSA's, the Task Force's "framework will characterize research being carried out by CFS establishments in the six eastern provinces." This Task Force reported in June 1979 (Runyon et al. 1983) and an Implementation Team was set up to work out organizational details; they reported in October of the same year. Any relationships between CANUSA's Activity Schedule and the program of the Implementation Team of the Task Force are unclear.

From the time when the Implementation Plan of the Implementation Team was established, the influence of CANUSA's Activity Schedule on eastern Canadian research was virtually nil. Under the 1977 Memorandum of Understanding a Joint Policy Program Council existed, as did a Joint Planning Unit, an Advisory Committee, and a Program Leader Canada. (Actually, the Advisory Committee was negated by a unilateral U.S. policy decision, Runyon et al. 1983). But then a Canadian Forestry Service program also existed, complete with the Implementation Plan that related directly to the Task Force and not necessarily to CANUSA's Activity Schedule. (In a verbal mixup CANUSA's Targets became Task Force Goals which were reorganized into the Implementation Plan's Activities; hence the smallest organizational units of CANUSA became the largest units of the Canadian Forestry Service.)

Outside of the Canadian Forestry Service, it is difficult to trace CANUSA's influence to see if CANUSA's objectives affected CANUSA's practice, but we were able to find at least one linkage. The Task Force noted (p. A20) that a group in Quebec (Comité de la Recherche sur la Tordeuse des Bourgeons de l'Épinette) was convened in 1978 in response to signing of the Memorandum, to identify areas in need of funding should finances become available from the CANUSA Program. The Task Force saw the Comité's approach as incompatible with that attempted by the Task Force.

An evaluation of CANUSA organization and administration by Runyon et al. (1983), noted that Canadian researchers outside of the Canadian Forestry Service did not participate in the Canadian phase of CANUSA because research support was not available to them. Some U.S.-CANUSA money was made available to Canadian researchers but U.S. control and reporting conventions did not generally stimulate potential Canadian applicants.

The CANUSA Mid-Program Report (Grimble 1981, p. 2) listed various Working Groups that were "organized to co-ordinate research activities by major subject area" for CANUSA-East. But Runyon et al. (1983) list their function as providing program management with advice on user and research needs, and on resource allocation recommendations to R&D activities. Perhaps it is not surprising that "there was considerable dissatisfaction and confusion among users and scientists as to their purpose" (Runyon et al. 1983, p. 8). Seven Working Groups are listed, not corresponding closely to the six Targets of the Activity Schedule. One Working Group was called "IPM Planning and Decision Modeling" and had co-leaders, one a Canadian. The influence of this Working Group on the evolution of budworm research along the lines of IPM planning and decision modeling in the Canadian Forestry Service, in terms of the Implementation Plan, was slight.

CANUSA's Mid-Program Report (Grimble 1981) lists studies related to each of the six Targets of the Activity Schedule. No Canadian work is cited with respect to Target 6. To find out what was happening it is useful to go back to the Task Force report.

The orientation of the Task Force was definite; we quote from its report:

> "In the past CFS research on the eastern spruce budworm has concentrated primarily on generating information on the spruce budworm which would permit the forest manager to solve the budworm/forest problem. There has been little or no attempt to focus the research in such a way it would *ensure* that forest managers were being provided with the information they require to make decisions."

Based on discussions with various relevant agencies in eastern Canada, the Task Force identified ten research Goals, but grouped the Goals into Goal Oriented Working Groups, each Group with its Group Leader. An Implementation Team considered the research Goals proposed by the Task Force, and provided to the Canadian Forestry Service directors, individual research projects and costing details relative to the broader research Goals. In their considerations the Implementation Team made some changes to the proposed Goal Oriented Working Group structure, and identified eight so-called Activity Groupings: Activity A through H. Activity leaders were named and the implementation process began.

The Task Force report was in some ways in step with thinking in CANUSA. Both believed in the value of models for helping with long-term management planning about the spruce budworm. Both believed that models are useful not only within well-defined disciplines but also between the relevant disciplines to "link these bits and pieces of scientific understanding into a logically consistent whole" (Canadian Forestry Service 1979, p. 71).

The Task Force suggested setting up of a core modeling group in one Canadian Forestry Service Research Centre, consisting of 3-4 modelers, to begin construction of a MFRC/UBC-type of model (Cuff and Baskerville 1983) to satisfy Goal 5. Once done so-called regional modelers would adapt this general model to their circumstances to satisfy Goals 4 and 6.

What is now referred to as Activity D included all of Goals 4, 5, and 6 in the Task Force report and was given the name "Impact requiring modeling." In the Implementation Plan report Goal 4 was split and part included in Activity A and part kept in Activity D. This change saw the "shorthand" name of the Activity modified to "Management Strategy." Both names reflect part of the nature of Activity D.

The objective of Goal 4 (2) — that part given to Activity D — according to the Implementation Plan report, was "To develop biologically-realistic models that will predict budworm populations and their impact in real time, for use over the medium term (10-yr) planning period." Two sub-objectives were also identified: the first was: "To determine key factors and processes in budworm population dynamics, and to incorporate these in a biologically-realistic predictive model." The second sub-objective was: "To determine the impact of budworm-caused defoliation on increment loss and mortality, and to incorporate these relationships in a biologically-realistic predictive model."

Goal 5 was, to quote from the Implementation Plan report: "To define tree and stand characteristics that determine susceptibility and vulnerability, and on this basis to develop a biologically-realistic simulation model that will permit the forest manager to explore long-term management options leading to a forest with low budworm risk."

Goal 6 moved away from the area of Budworm Impact to Budworm Management. It was stated by the Task Force report and Implementation Plan as follows:

"To cooperate with the provincial forest agencies in the building of models for the design and evaluation of alternative strategies for dealing with spruce budworm/forest problem."

Activity D of the Implementation Plan thus shared characteristics with Target 6 of CANUSA's Activity Schedule. In fact, a subdivision of Target 6 had only one relevant Activity for eastern Canada (Activity 6.1.3) and that was to develop and use the existing MFRC/UBC model so as to "Provide [a] SBW pest management system for application by various jurisdictional areas and management units" (McKnight and Buckner 1981, p. 43) at the end of CANUSA.

Activity D was led by C.A. Miller (of the Maritimes Forest Research Centre) until his retirement; A.W. Thomas took over temporary responsibility for Activity D, and in spring 1982 the job was passed to W.R. Cuff.

In describing the history of Activity D, we quote extensively from W.R. Cuff's December 1982 report to the CFS Spruce Budworm Management Committee, i.e., the Implementation Team:

> "In my opinion forces for change with respect to Activity D predate ... [Miller's] October 1981 report but my first realization of dissatisfaction came at a meeting of the Spruce Budworm Modelling Group held in Sault Ste. Marie, Ontario, during 19-21 January 1982. A report in CANUSA Newsletter 21 (March 1982) summarized the results of the meeting as follows:
>
>> 'The general conclusion of the meeting was that a holistic approach such as CANUSA-West is using is not as applicable to the eastern situation. There are no definable needs for such a model at this time; however, there are some specific needs for the individual models. The most "useful" model, in the east, is the tree model in that it tries to address the needs of the user groups. We still lack the knowledge of how to link the budworm model to the tree model.
>>
>> The group agreed that future meetings should be restricted to small groups with specific data needs.'
>
> "This report makes it clear that the sought-after "concensus on the elements of a biological forest/budworm model" was not to be. (This quote is from C.A. Miller's 1981 report to the C.F.S. Spruce Budworm Management Committee).
>
> "In fact the role envisaged by the Task Force for the M.F.R.C./U.B.C. model never did get off the ground ...
>
> "Miller's 1981 report to the C.F.S. Spruce Budworm Management Committee suggested that the arrival of the Core Modelling Group Leader would get progress along the track envisaged by the Task Force:
>
>> 'Cuff, the new core modelling leader at MFRC will arrive in October 1981. An analysis of all pending critiques of the policy model should commence shortly afterwards. With the incorporation of research results from the susceptibility-vulnerability and small larval dispersal studies, a major revision of the model's components and possibly its basic structure is anticipated'.
>
> "The envisaged analysis of the "policy" (M.F.R.C./U.B.C.) model did occur but the analysis went further than revision of the model. I went back to the 1978 Task Force for the Review of C.F.S. Research on the Eastern Spruce Budworm and studied the expectations for that model. There I found an undue emphasis on one form of model, a "simulation model", and an optimistic view on the leadership capabilities of comprehensive simulation models. And I found the following statement: "each model should be the best current hypothesis, with respect to dynamics in the part of the system it purports to mimic" (p. 71). This orientation might have been acceptable had there been room in the Task Force's scheme for stopping the development of the model when it was not scientifically possible to decide on the best current hypothesis, but there was no such room. Since the "best current hypothesis" is effectively given organizational approval, the potential for destructive power struggles among the proponents of competing hypotheses is obvious. I believe that it was the Task Force's emphasis on simulation models, the overly-optimistic view of the potential of comprehensive modelling, and power struggles initiated by the appearance of giving organizational approval to one scientific idea in each field covered by model processes that led to progress being made only in directions other than those anticipated by the Task Force report.
>
> "Working as Core Modelling Group Leader at M.F.R.C. under the Task Force scheme, I would have been faced with the same difficulties. This group was originally given the responsibility by the Task Force to familiarize themselves with the M.F.R.C./U.B.C. model and then begin work on a comprehensive simulation model relevant to Goal 5. The Task Force envisaged that as progress was made on the generalized Goal 5 model, so individual modellers were to be appointed in each of the C.F.S. regional laboratories to organize from the M.F.R.C./U.B.C. model and Goal 5

model the construction of regional models required to meet Goals 4 and 6, and hence guide research and forest management direction.

> "For a variety of reasons this scheme was not implemented. First: major modifications to the scheme are apparent in the 1979 Implementation Plan. Second: the anticipated increase in comprehensive simulation modelling staff in eastern C.F.S. laboratories did not occur. Third: I made it clear ... that I did not think it productive to think in terms of one modeller leading other scientists in the production of a single, all-encompassing model.
>
> "It is clear, then, that the overall scheme envisaged by the Task Force was quickly modified and then virtually slipped away from consideration ... it is clear that there is no C.F.S. staff member in place who is taking the initiative in resurrecting the original scheme ... I think the relevant job to do now is to look beyond the recommendations of the Task Force to see the forces or new perceptions that they were responding to, and to act accordingly.
>
> "Thus I will try in the rest of this section to distinguish between the simulation modelling tool ... and ... hopes for the tool. Models within established disciplines were seen to be of continuing value but the ... new tool was the comprehensive model: "models that link these bits and pieces of scientific understanding into a logically consistent whole" (p. 71). This tool was seen as useful to the designing of research towards the attainment of mid- and long-term forest management planning and to the formulation of forest management strategies."

In subsequent work as Activity D leader, W.R. Cuff aimed to encourage work along the lines of the problems specified in Goals 4(2), 5, and 6 with no methodological bias for Activity D participants. That is, simulation modeling — old or new — would be used only as participants were interested.

Thus, in the area of the integration of forest and pest management in eastern Canada, the evolution of the IPMS concept from, essentially, CANUSA's Target 6, Activity 6.1.3 occurred from perceptions and constraints from within the eastern provinces of Canada, particularly from within the Canadian Forestry Service. CANUSA was sent annual reports for inclusion in their Basic Record but no formal mechanism operated to get a CANUSA response.

To summarize: this discussion of objectives and practices of CANUSA in eastern Canada shows that objectives — in detail — were laid out, but in the Canadian Forestry Service, a competing chain of command left CANUSA with an information dissemination function for Canadian and U.S. workers on the spruce budworm. CANUSA's Target 6 did survive the Task Force and Implementation Plans, although with substantial refinement for the perceived needs of eastern Canada. But Goals 4(2), 5, and 6 of the Task Force subsequently were substantially modified as Activity D evolved. Thus as the CANUSA objectives relative to Target 6 were implemented in eastern Canada — as the practice occurred — so the objective itself was refined.

Are Forest and Pest Management Systems Compatible?

We saw above the diversity of forest management systems in place in eastern Canada. Similarities exist between the Ontario and New Brunswick forest management planning systems for Crown land. Spruce budworm survey and assessment techniques follow similar general procedures (Dorais and Kettela 1982). Otherwise the diversity of approaches is the striking feature of the planning systems.

The IPMs of CANUSA's Activity Schedule reflected no diversity: "information needed to meet Program objectives develops within activities and flows from one target to another, ultimately converging in Target 6 to provide resource managers a variety of action alternatives and guidelines, i.e., integrated pest management systems for spruce budworms" (McKnight and Buckner 1981, p. 2). The practice of research in the Canadian Forestry Service in eastern Canada during the life of CANUSA was more appropriately diverse, in part because the Task Force held discussions with all provinces in eastern Canada and in part because it proved unproductive to follow through with such a rigid and unitary form of R&D planning as reflected by the CANUSA Activity Schedule and the Task Force report.

To answer the question posed at the beginning of this section: no, there is not yet the appropriate diversity in pest management research and development to allow pest management to take its rightful role in forest management.

How Can Better Integration Be Achieved?

To end this paper on a negative note is to get nowhere. What did our CANUSA experience in the eastern provinces of Canada tell us about how we can better support our Canadian Forestry Service clients in the area of forest management?

Perhaps a first step along the line explored here for eastern Canada may be found in Simmons et al. (1984). There the authors considered the various levels of organization within which decision making occurs; the significance of these levels was emphasized in this report by describing experience in Operations Research application successes at operational and policy levels. Simmons et al. (1984) also advocated care on the part of the IPM(s) researcher to ensure that the system he develops is compatible with the "decision process in use by the forest industry/ management agency."

The essence of the points made by Simmons et al. (1984) is that the developer of IPM tools (the scientist) must be sensitive to the client's needs if the scientist wishes to see the work used. This is reminiscent of Mintzberg's (1980) plea for a return to open-end problem exploration rather than methodology advocacy. In a study of the available literature on problems with the implementation of models, Cuff and Walker (unpublished manuscript) found that positive suggestions tended toward two categories: make a usable model and involve the model user throughout the process. The former enables the work to be applied; the latter enhances the probability that the client will have sufficient commitment to the model that he will actually try to use it.

Gass (1983, p. 611) provides a definition of utility that clarifies our findings: "The "utility" of a model depends on its being useful and usable, and that it is used. A model can be considered *useful* if it shows promise of attaining the objectives initially established for it. A model can be considered *usable* if it is understandable and plausible to both technicians and policymakers, economic to solve in terms of data collection and computation, and accessible to those who wish to use it. Finally, if a model is useful and usable, it stands a good chance of being *used*, especially if potential users receive the proper training, supplemented by adequate documentation."

Although we would expand on the definitions to more fully reflect their significance, the terms useful, usable, and used are key words in applied science. To us they imply a careful analysis of not only the interests of the researchers but also those of the client. Both must be satisfied or "use" will not be obtained.

The Task Force restricted its discussions with client organizations to the level of management that evaluates the importance of potential budworm damage to the flow of wood and which frames the forest management actions in the broad sense. It was from these discussions that the recommendation arose for the development of a single, comprehensive simulation model, representing the "best current hypothesis," that could be used to guide research and forest management direction. At the time the discussions took place, in 1978, we have no reason to doubt the interest by participating forest managers for such a decision-aiding tool. However, this suggestion, as refined by the Implementation Plan led more toward tendencies of rhetoric and demoralization in the research scientists than to productive and directed research toward construction of the model. We put forward two reasons why the suggestion did not lead to productive research along the line envisaged.

First, there was confusion in the minds of many scientists over the role and nature of scientific knowledge in forest management practice. To list needs of forest managers is insufficient to organize research direction if the list contravenes scientific tradition; for example, a "best current hypothesis" assumption poses no difficulty to a forest manager used to choosing between various options in order to resolve some issue in a limited time frame. The same assumption, however, can pose a dilemma to a scientist if the time frame is shorter than the time needed to test the relevant hypothesis scientifically. To avoid such misunderstandings in the future it seems desirable that detailed consideration be given to the needs and perceptions of both the forest management clients and the research scientists.

Second, we believe that research direction is not effectively done simply by directing experimental programs toward elaborating one comprehensive simulation model; this method of directing research, set out in the Implementation Plan, is too neat, too systematic. Much opinion in such learned journals as Research Management favors the opposite approach to research direction — although not to development activities. In a recent article Frosch (1984) writes about R&D as follows:

> "To begin with, there is a "two cultures" problem. I call it the tidiness problem in R&D and manufacturing. The problem is that, by their very nature, research and the devising of innovative ideas are highly untidy processes. That is, research cannot be dealt with systematically, that is simply not the way in which people get ideas, or are stimulated to ideas. Research, particularly basic research, is done by people who have odd modes of thought, who work in ways that are strange to business, who are uncomfortable with precise time scales (although at times they can be driven by them), and who frequently will progress best by diverging strongly from what it was they originally said they were going to do.
>
> "At the other end of the process, if one is going to manufacture a million of something, or as in the NASA case, only one but it absolutely must work, there must be an extraordinary degree of tidiness of system, of detailed record keeping and of great planning. Somewhere in the middle a splice is being made from a process which from the point of view of the tidy manufacturing operator is so untidy and difficult as to be disreputable, and at the other end to something which should be so neat and preplanned that many of the research people find it intolerable. There is a cultural matching process which is involved in technology transfer."

As a general statement, it seems pertinent to suggest that individual research scientists take a positive attitude towards the client they are supporting, and set out to the best of their ability to help, while being concerned about their own interests and the limitation of science's contribution to forest management. Research managers will have an important role in this task. It has been said that the single most important point regarding technology transfer — or, as we call it in this paper, integration of forest and pest management — is that "it is a human process which must be engaged in by consenting adults" (Frosch 1984). Thus it is noteworthy that Runyon et al. (1983) used the words frustration, cynical, anxiety, extremely suspicious, and uncomfortable in describing the reaction of Canadian research scientists and forest managers to the CAN-USA program organization and administration. The emotions and attitudes that such words imply do not enhance communication between the research scientist and his forest management client. It seems there is an immediate challenge to research managers to contribute to the removal of barriers to fruitful communication between research scientists and forest management clients.

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Literature Cited

Armson, K.A.; Robinson, F.C.; Osborn, J.E. 1980. Forest management manual for the Province of Ontario. Ont. Minist. Nat. Resour., Toronto, Ont. 132 p.

Bakus, G.J.; Stillwell, W.G.; Latter, S.M.; Wallerstein, M.C. 1982. Decision making: with applications for environmental management. Environmental Management 6(6):493-504.

Baskerville, G.L. 1983. Approaches to the spruce budworm problem in Nova Scotia and New Brunswick. Pages 73-81 *in* C.J. Sanders and J.R. Carrow, co-chairmen. The spruce budworm problem in Ontario: real or imaginary. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. COJFRC Symp. Proc. O-P-11. 116 p.

Baskerville, G.L.; Montgomery, B.A. 1983. Spruce budworm information leaflets for the Lake States. V. Forest management. Mich. Coop. For. Pest Manage. Prog., East Lansing, MI. Leaflet 83-11. 2 p.

Baskerville, G.L.; Weetman, G.F. 1978. Forest management at Nova Scotia Forest Industries Ltd. Case Study 1. Pages 1-1-1-27 *in* F.L.C. Reed & Associates Ltd., eds. Forest management in Canada. Vol. II. Case Studies. Can. For. Serv., For Manage. Inst., Ottawa, Ont. Inf. Rep. FMR-X-103. 177 p.

Belzile, H. 1981. Improvements in the status of Quebec's private forest over the past ten years. Pages 15-22 *in* M. Lortie, coord. Proc. Symp. on eastern Canada small private land forestry, 27-29 October, 1981. Faculté de foresterie et de géodésie, Univ. Laval, Ste-Foy, Que. 110 p.

Bonnor, G.M. 1982. Canada's forest inventory 1981. Can. For. Serv., For. Stat. Syst. Br., Chalk River, Ont. 79 p.

Canadian Forestry Service. 1974. The role and policy of the Canadian Forestry Service. Can. For. Serv., Prog. Dev. Br., Ottawa, Ont. 18 p.

Canadian Forestry Service. 1979. Report of the Task Force for the review of the Canadian Forestry Service Research Program on the eastern spruce budworm. Can. For. Serv., Ottawa, Ont. 83 p. plus Appendices.

Canadian Forestry Service. 1984a. Canada-New Brunswick Forest Renewal Subsidiary Agreement. Canada Dep. Environ/New Brunswick Dep. Nat. Resourc. Can. For. Serv., Ottawa, Ont. 28 p.

Canadian Forestry Service. 1984b. Summary of work plans 1984-85. Can. For. Serv., Ottawa, Ont.

Carrow, J.R. 1983. Spruce budworm spraying — Ontario's approach. Pages 67-71 *in* C.J. Sanders and J.R. Carrow, co-chairmen. The spruce budworm problem in Ontario: real or imaginary. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. COJFRC Symp. Proc. O-P-11. 116 p.

Conner, J.T. 1976. Status and prospects for use of modeling in integrated pest management. Pages 227-229 *in* R.L. Tummala, D.L. Hayes, and B.A. Croft., eds. Modeling for pest management: concepts, techniques, applications U.S.A./U.S.S.R.

Cuff, W.; Baskerville, G. 1983. Ecological modelling and management of spruce budworm infested fir-spruce forests of New Brunswick, Canada. Pages 93-98 *in* W.K. Lauenroth, G.V. Skogerboe, and M. Flug., eds. Analysis of ecological systems: state-of-the-art in ecological modelling. Developments in environmental modeling 5, Elsevier, Amsterdam. 992 p.

Dorais, L.; Kettela, E.G. 1982. A review of entomological survey and assessment techniques used in regional spruce budworm, *Choristoneura fumiferana* (Clem.), surveys and in the assessment of operational spray programs. Eastern Spruce Budworm Council, Fredericton, N.B. 43 p.

Ford-Robertson, F.C., ed. 1971. Terminology of forest science, technology practice and products. The Multilingual Forestry Technology Series No. 1. Soc. Am. For., Washington, D.C. 349 p.

Franz, J.M. 1976. Towards integrated control of forest pests in Europe. Pages 295-308 *in* J.F. Anderson and H.K. Kaya, eds. Perspectives in forest entomology. Academic Press, New York. 428 p.

Frosch, R.A. 1984. R&D choices and technology transfer. Res. Manage. 27(3):11-14.

Gass, S.I. 1983. Decision-aiding models: validation, assessment, and related issues for policy analysis. Operations Research 31(4):603-631.

Giesen, M.O.; Radford, K.J. 1983. Strategy and tactics: a new model for organizational decision making. Infor. 21(1):52-60.

Grimble, D.G. 1981. CANUSA mid-program report. U.S. Dep. Agric., For. Serv., Northeastern For. Exp. Stn., Broomall, Pa. 13 p.

Hall, T.H. 1978. Toward a framework for forest management decision making in New Brunswick. New Brunswick Dep. Nat. Resour., Fredericton, N.B. Rep. No. TRI-78 83 p.

Hardy, Y. 1978. Integrating the spruce budworm in Quebec forest management. Pulp & Paper Canada 79(1):77-79.

Irving, H.J.; Webb, F.E. 1981. Forest protection against spruce budworm in New Brunswick. Pulp & Paper Canada 82(1):23-31.

Johnson, W.L. 1981. The G.D.A. Incentive Program for Private Landowners in Nova Scotia. Pages 1-5 *in* M. Lortie, coord. Proc. Symp. on eastern Canada small private land forestry, 27-29 October, 1981. Faculté de foresterie et de géodésie, Univ. Laval, Ste-Foy, Que. 110 p.

Jones, D.D. 1979. The budworm site model. Pages 91-155 *in* G.A. Norton and C.S. Holling, eds. Pest management. Proc. Int. Conf., 25-29 October, 1976. Pergamon Press, Oxford. 349 p.

Leblanc, P. 1981. Is the freedom of choice for the private woodlots in New Brunswick in jeopardy? Pages 6-14 *in* M. Lortie, coord. Proc. Symp. on eastern Canada small private land forestry, 27-29 October, 1981. Faculté de foresterie et de géodésie, Univ. Laval, Ste-Foy, Que. 110 p.

Lortie, M. 1984. Forest policy development in Quebec. For. Chron. 60:67-70.

Lussier, L. 1976. The forest management plan operation in Quebec. Pulp & Paper Canada 77(7):42-51.

McKnight, M.E.; Buckner, C.H. 1981. CANUSA Program Activity Schedule: Master plan for coordination and cooperation. U.S. Dep. Agric., For. Serv., Washington, D.C. 46 p.

Millar, V.E. 1984. Decision-oriented information. Datamation January, 1984. Pages 159-162.

Mintzberg, H. 1980. Beyond implementation: an analysis of the resistance to policy analysis. Infor. 18(2):101-138.

Mumford, J.D.; Norton, G.A. 1984. Economics of decision making in pest management. Ann. Rev. Entomol. 29:157-174.

Munro, J.; Burton, E.; Dickson, W.; Mercer, R. 1979. Report of the committee on the economic impact of spruce budworm in Newfoundland. Can. For. Serv., Newfoundland For. Res. Cent., Inf. Rep. N-X-170. 23 p.

New Brunswick Department of Natural Resources. 1982. Forest Management Manual. Dep. Nat. Resourc., For. Manage. Br., Fredericton, N.B.

New Brunswick Private Woodlot Resources Study. 1983. Private woodlots: what does the future hold? New Brunswick Research and Productivity Council, Fredericton, N.B. 119 p.

Ontario Ministry of Natural Resources. 1982. Private land forests, a public resource. Ont. Minist. Nat. Resour., Toronto, Ont. 161 p.

Ornstein, R.F. 1972. The psychology of consciousness. San Francisco: Freeman.

Ostaff, D. 1982. The history of Plot 314-A: a prelude to destruction. Can. For. Serv., Marit. For. Res. Cent., Fredericton, N.B. Tech. Note No. 55.

Paré, G. 1983. The spruce budworm in Quebec: the situation today. Pages 83-87 *in* C.J. Sanders and J.R. Carrow, co-chairmen. The spruce budworm problem in Ontario: real or imaginary. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. COJFRC Symp. O-P-11. 116 p.

Reed, F.L.C. and Associates Ltd. 1978. Forest Management in Canada. Vol. 1. A study to improve the basis for policy formulation, planning, and practice in intensive forest management. Can. For. Serv., For. Manage. Inst., Ottawa, Ont. Inf. Rep. FMR-X-102. 155 p.

Roberts, J. 1980. The hyper-rationality trap explained? Infor. 8(4):364-366.

Ruesink, W.G. 1976. Status of the systems approach to pest management. Ann. Rev. Entomol. 21:27-44.

Runyon, K.; Lachance, D.; Coster, J.; Knauer, K. 1983. CANUSA spruce budworm: program organization and administration effectiveness. U.S. Dep. Agric., For. Serv., Washington, D.C. 18 p. plus Appendices.

Simmons, G.A.; Cuff, W.; Montgomery, B.A.; Hardman, J.M. 1984. Integrated Pest Management. Chap. 2 *in* D.M. Schmidt, D.G. Grimble, and J.L. Searcy, tech. co-ords. Managing the spruce budworm in eastern North America. U.S. Dep. Agric., For. Serv., Washington, D.C. Agric. Handb. No. 620.

Smyth, J.H.; Nausedas, I.A. 1982. Rural land and landowners of Ontario: a private land forestry perspective. Canada-Ontario Joint Forestry Research Committee. Ont. Minist. Nat. Resourc., Toronto, Ont. 97 p.

van Fraassen, A.M. 1983. Pages 57-60 *in* C.J. Sanders and J.R. Carrow, co-chairmen. The spruce budworm problem in Ontario: real or imaginary. Can. For. Serv., Great Lakes For. Res. Cent., Sault Ste. Marie, Ont. COJFRC Symp. O-P-11. 116 p.

Waters, W.E.; Stark, R.W. 1980. Forest pest management: concept and reality. Ann. Rev. Entomol. 25:479-509.

Webb, F.E.; Irving, H.J. 1983. My Fir Lady: The New Brunswick production with facts and fancies. For. Chron. 59:118-122.

Whalon, M.E.; Croft, B.A. 1984. Apple IPM implementation in North America. Ann. Rev. Entomol. 29:435-470.

Winget, C.H. 1984. The federal role in forest management: the continuing quandary. For. Chron. 60:177-179.

Integration of Forest and Pest Management: Implications for Forest Management — The Western View

A.R. Stage

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Forest management and pest management are "integrated" when decisions to devote resources to the two functions compete in the same arena and are judged by the same standards. Integration requires the "world views" of managers and scientists in the two functions to be congruent. This congruency implies a similar hierarchical structure of their respective inventory, modeling, and decision procedures. The convergence to the common world view required for integration requires compromise from all parties. Benefits are more efficient use of resources and — presumably — fewer pest problems. How to represent uncertainty in the resource modeling and decision process remains a barrier to integration in long-range (strategic) planning.

On intègre l'aménagement forestier et la lutte contre les ravageurs lorsque les décisions concernant l'affectation des ressources à ces deux activités se heurtent sur le même plan et sont prises en fonction des mêmes normes. L'intégration exige que, sur le plan mondial, les avis des aménagistes et des scientifiques sur les deux activités s'harmonisent. Cette harmonie implique une structuration hiérarchique similaire de leurs inventaires, de leurs modèles et de leurs prises de décisions respectifs. La convergence nécessaire à l'intégration exige que toutes les parties fassent des compromis. Les avantages en sont une utilisation plus efficace des ressources et, présumément, moins de problèmes causés par les ravageurs. La part à accorder à l'incertitude, en modélisation des ressources et dans la prise de décisions, reste un obstacle à l'intégration en planification à long terme (stratégique).

Introduction

In the discussion at these proceedings of integration of pest management and forest management, no one has yet stated just what integration is, or why it is to be sought. How can we recognize whether these two disciplines have been "integrated" without a clear definition? Here is mine. Because management is the process whereby resources are allocated so as to attain the goals of the manager, it follows that integration for forest and pest management has been achieved when:

- managers of the forest and managers of the pests inhabiting that forest share common goals.
- decisions to invest in activities in the two functions compete for common resources in the same arena and are judged by the same standards.

In this context, it does not matter whether the decision-maker operates intuitively, rationally, or hyper-rationally (Cuff 1985).

The first of these conditions, common goals, has received considerable attention in recent years (Stark 1978, Waters 1976). So successful has been their argument that one is belaboring the obvious to insist that "integrated pest management" cannot occur without having found the "user's bottom line." What has not been so clear is that the users must be willing to restructure some of their "upper lines" if they are to improve their management.

Benefits of integration really follow from achieving the additional condition specified in the second condition — "competing in the same arena." When alternative allocations of resources are considered jointly, the marginal benefits of the selected pest management activities will be more nearly equal to the marginal benefits for other silvicultural activities. This equality of benefits from marginal activities is required to achieve an optimal mix of activities. If the benefits can be measured in dollars, then the mix is economically optimal. If the returns can only be evaluated subjectively, at least the subjectivity shares the same biases and value system for all alternatives.

Silviculture and pest management can interact either synergistically or antagonistically as has been amply described elsewhere in these proceedings. In either case, their combined effects must be analyzed simultaneously. Otherwise, decisions reached independently must always be less effective than decisions based on simultaneous evaluation of effects.

Even where desired by all concerned, integration of these two disciplines will not just happen. The "world view" of the managers and the research scientists in each of the disciplines must be congruent. Thus there are four actors involved — forest and pest managers and their research counterparts. Furthermore, their "world views" must feature ecosystem units that are biologically meaningful. Small wonder that integration takes effort!

I deliberately use the term "world view" rather than "model." By "world view" I mean the whole mental set or paradigm with which a trained specialist organizes his knowledge of the world. By contrast, a model is a very explicit but much less rich abstraction of this "world view."

Activities competing for resources in a common arena are chosen according to *differences* in their expected utility for reaching the management goals. Therefore, if expected utility is estimated for one set of activities — say thinning — on a scale of next-decade-allowable-harvest, then all activities that affect the same biological processes as thinning should be evaluated on that scale. Furthermore, the same model should be used to estimate the effects (Figure 1). For example, if one of the utilities for which a forest is managed is wildlife habitat, then effects of thinning, planting, and pest suppression on wildlife habitat should be estimated by the same model. To do otherwise would very likely lead to estimates of *differences* that are largely the differences in the biases of the several models rather than the differences in the true effects of the competing activities.

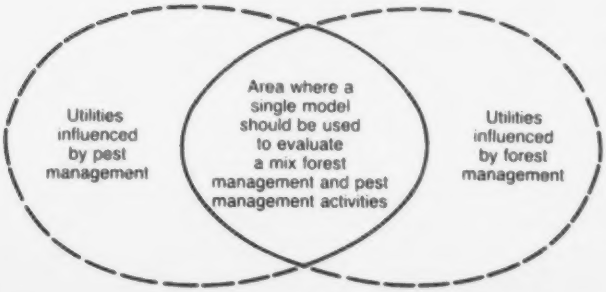

Utilities influenced by pest management
Area where a single model should be used to evaluate a mix forest management and pest management activities
Utilities influenced by forest management

Figure 1. Where forest management and pest management affect the same utilities, a common model should be used.

In addition, each decision-maker brings to the task a different set of biases and attitudes toward risk and uncertainty. Therefore, no matter how precise future effects may be estimated, different managers may reach different decisions confronted by the same "objective data." The same reasoning that leads me to require consistency in the modeling also requires a consistency in the "world view" of the decision-maker that can only be achieved by having both pest and forest management decisions arrived at by the same managers.

One should not conclude that I am recommending that all pest management and forest management decisions must be made in the same arena or be judged by the same standards. In other words, total integration of pest management and forest management is neither necessary nor desirable. But when the same utilities are influencing decisions, it seems silly to do otherwise!

Why the Dichotomy?

Forest managers have been using volume regulation since at least 1422 (Roth 1914). Because volume regulation requires an estimate of future growth, we can claim that forest managers have been using some form of a model for half a millennium. And their use of the yield table, which was their model, included an allowance for losses to pest damage, disease, and wind. Why, then, do we now have a dichotomy that calls for integration of pest management with forest management?

In my view, the dichotomy can be traced to the point where we attempted to insert the science of growth and yield into the basis for forest management decisions. For at that point, yield tables constructed to represent yield *potential* replaced empirical yield tables based on extensive experience. Although the basis of the yield table changed, the ritual of forest decision-making did not. Thereafter, forest plans were based on potential yield, at least for the contribution from newly regenerated stands. In this context, the role of the pest manager was to keep the forest free of pests so that the potential could be achieved. Whether this objective was — or ever would be — attainable may have been discussed in many pest management colloquia, but the answer has only recently been woven into silvicultural decision-making.

During the schism, which started sometime in the 1920s, the abstractions that define the world view of the forest and pest manager also drifted apart. As the science of sampling became accepted, managers inventoried their forests with widely scattered points. At each point, they described the forests according to the arguments of their yield tables: site index and age, and — as yield science progressed — they added density. Pest managers, on the other hand, saw the forest as expanses of complex mosaics characterized by degree of defoliation or densities of "red tops," changing only in response to weather, contagion, and spray operations. The intersection of these two world views was practically empty. Where the forest manager had inventory plots, the pest data were scanty, and vice versa. Therefore, analysis of joint effects was precluded.

Methods of forest regulation being followed by managers also limit integration. Forests lacking large volumes of old growth are commonly regulated by area control. Rather than specifying periodic harvest volumes, area control calculates the fraction of the area to be harvested in each period as the ratio of period length to rotation length. In turn, rotations are determined by reference to estimates of potential yield. Actual volume production in these regions was — and is — monitored by comparing growth to removals. Only recently have the deficiencies of this approach been realized (Roach 1976). Because this consideration of growth-to-removals is meaningful only for large areas, pest managers were led to describe pest effects as growth reductions aggregated to similarly large areas. Integration is not possible, however, because the silvicultural activities are evaluated by their effects on rotation-years, while pest management activities are evaluated as a saving in periodic growth totaled over some unspecified collection of age-classes.

Let me illustrate from past experience with an assignment that would have linked pest impacts with very broadscale analysis of the timber resources of the United States. In the early 1960s, the Forest Service of the U.S. Department of Agriculture was in the midst of one of its periodic reviews of the nation's timber resources. One of the tasks was to estimate the benefits to be derived from pest management for a few major pest examples. The growth and yield forecasting system selected for the analysis was the TRAS system (Larson 1970). In TRAS, very large geographic regions, say northern Idaho, were represented by a stand table showing numbers of trees by 2-inch diameter classes. Rates of diameter increment, mortality, and removals were entered into the system based on empirical sample data from the population to be projected. There was no possible way to use the scientific knowledge of growth and yield in this system. Nevertheless, the projection system worked reasonably well because it did use a very extensive empirical data base.

In the world view of the yield scientists of the 1960s, forests consisted of even-aged stands of one or a few species that could be characterized by site index, age, and basal area. Unfortunately, forests corresponding to their world views included something less than 25 percent of forested lands, whereas the resource analysts had to represent all the forests. Hence their total reliance on empiricism.

When we approached entomologists to introduce an example of benefits that might follow from reducing mountain pine beetle impacts on lodgepole pine, we were stymied. Our growth and mortality data were for 2-inch diameter classes that encompassed all of northern Idaho. Therefore, the entomologists were requested to show how pest management would reduce beetle-caused mortality rates for those same classes. The entomologists just walked off in disgust — and rightly so!

The difficulty was that the model representing the world view of the resource analysts was incongruent with the world views of both the growth and yield scientists and of the entomologists.

Also, at about the same time, forest managers in several regions of the Forest Service were developing stand examination procedures to be used for silvicultural prescriptions (USDA Forest Service 1962). In the northern Rocky Mountains, stands contain a diversity of species, age, and condition classes because of effects of previous pest damage and partial cutting. Therefore, the stand prescriptions appropriate for a particular stand required a fairly detailed stand examination. It was to evaluate alternative stand treatments in this management and ecological environment that we developed the Prognosis Model for Stand Development (Stage 1973, Wykoff et al. 1982).

In addition to within-stand relationships, spatial relationships between stands also are important for evaluating the effects of management on several utilities influencing decisions. Pest contagion, watershed protection, and aesthetics all depend on how stand conditions differ within geographic units larger than a single stand. To accommodate these interpretations, we designed an inventory procedure in which the sample units were aggregates of adjacent stands (Stage and Alley 1972).

Although this procedure has been used to inventory all National Forests in Region 1, for timber planning, the capabilities of this design to represent spatial relations have seldom been utilized. This failure is probably due to the lack of models of resource response and the lack of planning models designed to use the spatial information.

Uncertainty As a Barrier to Integration

How managers and scientists view uncertainty remains a major barrier to integration. Scientists are most comfortable with cause-and-effect relationships, and hence are reluctant to approve models that are not deterministic. Managers, in turn, expect deterministic models. Indeed, most of the optimization models they use assume that the yield or production functions are deterministic. Unfortunately, natural systems contain a large measure of random, unpredictable variation!

When managers consider activities that differ in their chances of future pest damage, it is not too hard to convince these managers that differences in expected benefits should guide their decisions. In this application, expected value is used in the sense of Descartes, calculated by weighting the value of each outcome by its probability of occurring. Such is the world view common to many scientists following Descartes.

When an uncertain event such as an insect epidemic is far off, or is likely to occur anytime in a wide span of time, forest managers have a different view of how to deal with the uncertainty. In this case, they base their production decisions on estimates of potential yield. Then, when the epidemic happens, they take short-term actions to minimize their losses. Politicians appropriating funds for pest management follow a similar pattern. That these decisions seem irrational to scientists illustrates how far apart are the world views of managers and politicians from those of the "scientists."

The managers' rationale is convincing. By basing harvest levels on potential yield, they increase present income. If the future epidemic is inevitable, then reducing present harvests based on a reduced estimate of yield only leaves more trees for the bugs to kill. Harvest level is not perceived as having any effect on the probability of distribution of the epidemic. Indeed, if there is any truth to the view that "The quicker we get the forest under management, the sooner our pest problems will be solved," then using expected value yield estimates would lead in the wrong direction!

Unfortunately, present-day methods for resource allocation combine the task of comparing different silvicultural regimes with the task of calculating harvest schedules. Yet the methods must use the same yield estimates for both purposes.

We need to resolve this fundamental discrepancy of views. Until we do so, no amount of "user involvement," "user-friendly" packaging, nor public relations will fully integrate pest management with resource decision-making.

Implications for Management

These experiences have had a major influence on the direction of our research on quantitative analysis of forest resources in the northern Rocky Mountains. From it, I have tried to distill some principles applicable to "integration" of biological and managerial sciences. I propose these principles as the "implications for forest management" phrase in the title of this paper.

1. The "world views" of the several disciplines must share a set of common, natural entities arranged in a nested hierarchy. For example, trees within stands within watersheds within working circles, and so on. Furthermore, successive levels should be chosen so that a unit at the higher level represents the scope of the dynamic interactions among individuals at the next lower level. TRAS, as applied in the northern Rocky Mountain resource analysis erred by going from the tree level to the state level, skipping the stand level (and other levels as well). We knew that as basal area per acre increased, growth rates should decrease and mortality increase, but there was no way to estimate by how much because the stand level of integration had been omitted.

2. The units defined for each level in the system should correspond to the units treated by the activities whose effects are to be simulated. TRAS erred here, too, because we do not harvest a 2-inch diameter class in the whole of northern Idaho; we harvest by stand (but perhaps unwisely by diameter class within stand). Similarly, the UBC budworm model may have been deficient according to this criteria because silvicultural decisions usually address stands rather than the much larger cells used to subdivide the forest in that model.

3. Models representing the responses of the ecological system should be kept separate from the optimization models purporting to show how we ought to manage that system. The ecological response models can — and should — serve both the long-range and the short-range decision processes. But the optimization models for these two time spans will be quite different. However, if both levels of planning use the same biological assumptions, then the long-range plans can be decomposed into an attainable short-range schedule of activities.

4. The role of uncertainty in the decision process should be a major criterion guiding the design of models supporting that decision. Activities that do not modify chances of future epidemics may require a different kind of model than those activities that change the chances.

While abiding by these principles may reduce the barriers to integration, they are not sufficient. It remains for top-level managers to determine when integration is needed. Then, the manager can ensure that both forest management and pest management decisions compete for common resources in the same arena and are judged by the same standards.

Literature Cited

Cuff, W.; Walker, H.D. 1985. Integration of forest management and pest management in the eastern provinces of Canada. Pages 443-464 *in* C.J. Sanders, R.W. Stark, E.J. Mullins, and J. Murphy, eds. Recent advances in spruce budworms research. Proc. CANUSA Spruce Budworms Research Symp., 16-20 Sept., 1984, Bangor, ME. Can. For. Serv., Ottawa, Ont.

Larson, R.W.; Goforth, M.H. 1970. TRAS a computer program for the projection of timber volume. U.S. Dep. Agric., For. Serv., Washington, D.C., Agric. Handb. 377, 24 p.

Roach, B. 1976. Stocking levels — guides and fit to management plan. Pages 44-88 *in* Proceedings of the National Silviculture Workshop, Oct. 13-15, 1976, Eugene, OR. Div. of Timber Management, U.S. Dep. Agric., For. Serv., Washington, D.C.

Roth, F. 1914. Forest Regulation. Geo. Wahr, publisher, Ann Arbor, MI. 239 + viii p.

Stage, A.R.; Alley, J.R. 1962. An inventory design using stand examinations for planning and programming timber management. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn., Ogden, UT; Research Paper INT-126. 17 p.

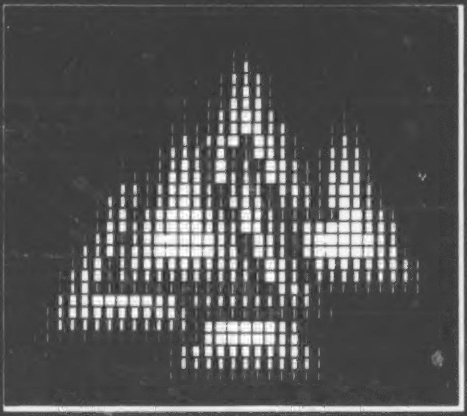
Stage, A.R. 1973. Prognosis Model for stand development. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn., Ogden, UT; Research Paper INT-137. 32 p.

Stark, R.W. 1978. Forest Management and integrated pest management. Pages 34-40 *in* R.D. Gale, ed. Proceedings for integrated pest management colloquium. Grey Towers, Milford, PA. U.S. Dep. Agric., For. Serv., Washington, D.C. Gen. Tech. Rep. WO-14, 76 p.

USDA Forest Service. 1962. Developing the data framework for effective timber management. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn., Ogden, UT; Misc. Publ. 25; 13 p.

Waters, W.E. 1976. Evaluation of insect impacts on forest productivity and values. Pages 15-18 *in* D.L. Kilbee, ed. The bases for integrated pest management. Proceedings of Plenary Symposium of IUFRO Congress Group 6 IUFRO XVI World Congress, Oslo, Norway, 24 June 1976; 28 p.

Wykoff, W.R.; Crookston, N.L.; Stage, A.R. 1982. User's guide to the stand prognosis model. U.S. Dep. Agric., For. Serv., Intermountain For. and Range Exp. Stn., Ogden, UT; Gen. Tech. Rep. INT-133. 112 p.



Part V

Invitational Panel

How successful have
we been in achieving
the goals of the
CANUSA Program?
In meeting the needs
of Forest Management?
What remains to be done?

Invitational Panel Summary

C.R. Blomquist

USDA Forest Service, Eastern Region, Timber Management, Milwaukee, Wisc.

To wrap up the symposium a panel was assembled to broadly represent the nonresearch community; to speak for forest management decision makers and give some feedback on the program. Program organizers were interested in the questions: How successful had program management been in achieving the goals of the CANUSA Program and meeting the needs of forest management?; and, what remains to be done?

The panel was diverse, representing Canada and the USA, East and West, industry and government. Each member represented a different user group. It was from that perspective they were asked to respond to CANUSA management's questions.

Presentations varied as widely as the backgrounds of the panel members, yet the common threads were significant. It was acknowledged that the CANUSA Program was not just a research effort, it also included development and technology transfer; there was a research effort underway before CANUSA on which to build; and substantial progress had been made during the intensified effort. There was disappointment expressed at the small amount of user involvement at the outset of the program. Each panel member cited specific results already in use and others that were very promising. Mentioned were such examples as the development of stand risk rating systems, monitoring techniques that look very promising, including the use of pheromones, promotion of *Bacillus thuringiensis* as a viable insecticide, refinements of silvicultural techniques.

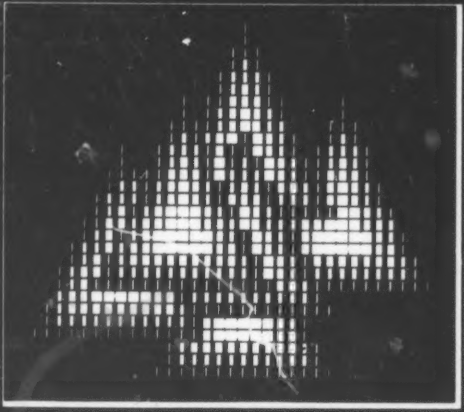
Concluding with answers to the question "What remains to be done?", there was unanimous agreement that the communication channels that have been developed must be kept open. Communication between scientists with common interests is important, but in order to get research into practice (many studies are just being completed) continued attention must be paid to the needs of forest managers. Transfer of technology will remain an important need. Effects of much of the research are long-term in nature so feedback from users and evaluation will not be possible for several years.

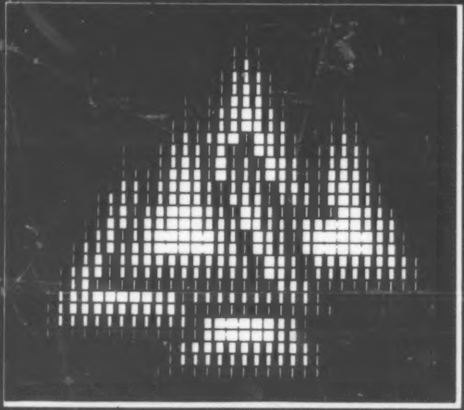
Research will not come to a halt when the CANUSA Program ends. Some ideas mentioned for continued research are:

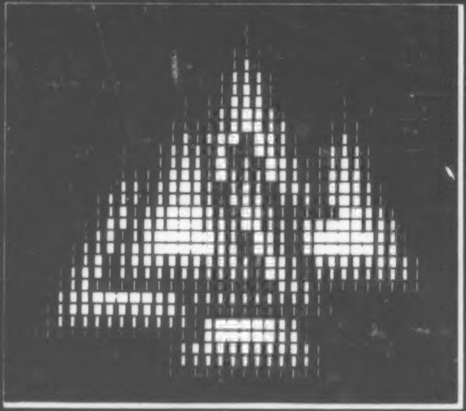
- Need for utilization technology to keep pace with the changing resource.
- Growth and yield and stand dynamics.
- Improve promising monitoring and prediction techniques.
- Forest protection needs continued attention, including improved efficacy of insecticides and application technology.
- There must be continued monitoring to determine effectiveness of silvicultural strategies.

The probable list of specific studies is unknown, but it would be extensive. No doubt there are areas of need that have not been mentioned. There was opportunity for audience participation but no significant additional input resulted from the discussions.

Members of the Invitational Panel were:
Chairman: C.R. Blomquist, USDA Forest Service, Eastern Region, Timber Management, Milwaukee, Wisconsin
Participants:
J.C. Mercier, Associate Deputy Minister, Canadian Forestry Service, Ottawa, Ontario
W. Maahs, District Manager, Timberlands International Corp., Milltown, Montana
W.M. Ciesla, Director, USDA Forest Service, Methods Applications Group, Fort Collins, Colorado
R.B. Anderson, Commissioner, Maine Dept. of Conservation, Augusta, Maine
J. Williams, Coordinator-Spruce Budworm Silviculture, International Paper Company, Augusta, Maine
J.R. Carrow, Assistant Deputy Minister, Department of Natural Resources, Fredericton, New Brunswick







Part VI

Poster Abstracts

Managing Forest Birds to Prevent Western Spruce Budworm Outbreaks

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and M.M. Lawless**

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Recent work has shown that predation by birds and ants is a major factor suppressing western spruce budworm (*Choristoneura occidentalis* Freeman) populations at sparse to moderate densities. The impact of bird predation on budworm populations can be increased in many stands through careful selection of cutting practices, management of snags and understory vegetation, and provision of nest boxes or other essential habitat requirements, such as water sources. Whole forests might be protected from budworm outbreaks by application of the most cost-efficient of these methods to moderately susceptible stands, and application of the most intensive to highly susceptible stands. The need for and economic potential for application of these methods will increase as forests become more homogeneous in species composition because of intensive management for maximum productivity of wood fiber.

Des travaux récents ont montré que les fourmis et les oiseaux contribuaient beaucoup à abaisser les populations de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) à des densités faibles à moyennes. L'action des oiseaux peut être augmentée, dans beaucoup de peuplements, par la sélection attentive des méthodes de coupe, par l'aménagement des chicots et de la végétation du sous-étage, et par l'installation de maisons d'oiseaux et d'autres facteurs essentiels de l'habitat tels que les points d'eau. Des forêts entières pourraient être protégées contre la tordeuse par l'utilisation des plus rentables de ces méthodes dans les peuplements moyennement vulnérables et l'utilisation des méthodes les plus intensives dans les peuplements les plus vulnérables. Plus les forêts deviendront homogènes à cause de l'aménagement intensif qui cherche à produire le maximum de fibres ligneuses, plus ces méthodes se révéleront avantageuses sur le plan économique.

Destruction and Consumption of Host Foliage by the Western Spruce Budworm

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Current growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and Englemann spruce (*Picea engelmannii* Parry) was fed to sixth instars of the western spruce budworm (*Choristoneura occidentalis* Freeman) in the laboratory. All larvae were reared individually in lamp-chimney cages at 22°C with a 12/12 photoperiod. Destruction and consumption of foliage were determined by ovendry weight. To prevent injury, fresh pupal weights were obtained 24 hours after pupation.

Mean consumption by males ranged from 173 mg on grand fir to 226 mg on subalpine fir. Consumption by female larvae ranged from 292 mg on Douglas-fir to 394 mg on subalpine fir. The last instar of the budworm is efficient under laboratory conditions, but both sexes destroyed 1.3 to 1.7 times more foliage than they ate.

On a nourri au laboratoire, des larves du 6^e^ stade de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) avec du feuillage de l'année courante de douglas taxifolié (*Pseudotsuga menziesii* [Mirb.] Franco), de sapin grandissime (*Abies grandis* [Dougl.] Lindl.), du sapin subalpin (*Abies lasiocarpa* [Hook.] Nutt.) et de l'épinette d'Engelmann (*Picea engelmannii* Parry). Toutes les larves étaient gardées dans des cages individuelles de verre de lampe, à 22°C, en photopériode de 12 heures. La destruction et la consommation du feuillage ont été déterminées à partir du poids anhydre. Pour éviter qu'elles soient blessées, les chrysalides ont été pesées à l'état frais, 24 heures après la chrysalidation.

Chez les mâles, la consommation moyenne variait de 173 mg de sapin grandissime à 226 mg de sapin subalpin; chez les femelles, de 292 mg de douglas à

The general pattern of foliage consumption was grand fir <Douglas-fir <spruce <subalpine fir.

Mean fresh pupal weights ranged from 83 to 109 mg for males and from 109 to 142 mg for females. Spruce and subalpine fir produced the heaviest pupae of both sexes. Weights of experimental pupae were similar to those of pupae collected in the field from the same host, indicating that the rate of consumption of foliage by the experimental larvae approximates rates in nature.

394 mg de sapin subalpin. Dans les conditions de laboratoire, le dernier stade larvaire de la tordeuse est efficace, mais les deux sexes ont détruit de 1,3 à 1,7 fois plus de feuillage qu'ils n'en ont mangé. Le feuillage a généralement été consommé dans l'ordre croissant suivant: sapin grandissime, douglas taxifolié, épinette, sapin subalpin.

Chez les mâles, la masse moyenne fraîche des chrysalides variait de 83 à 109 mg, chez les femelles de 109 à 142 mg. L'épinette et le sapin subalpin ont donné les chrysalides les plus lourdes, chez les deux sexes. Les masses des chrysalides étaient similaires à celles des chrysalides capturées dans la nature, sur le même hôte, ce qui montre que la consommation en laboratoire est à peu près la même qu'en liberté.

Sampling Hibernating Western Spruce Budworm and Estimating Survival During the Early Instars

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Methods of collecting hibernating western spruce budworm (*Choristoneura occidentalis* Freeman) larvae from Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were compared for accuracy and practicality. Within-tree patterns of occurrence of larvae hibernating on main stems and branches of Douglas-fir, western larch (*Larix occidentalis* Nutt.), and ponderosa pine (*Pinus ponderosa* Laws.) were studied. Sampling designs for estimating larval density on trunks, branch stems, and foliated twigs of Douglas-fir were derived. Survival from the egg stage through spring emergence was estimated on two plots in north-central Washington.

Recovery of hibernating larvae from Douglas-fir branch stems by attracting them to light was 88 percent. Recovery by extracting with sodium hydroxide and benzene was 74 percent.

Highest densities of hibernating larvae occurred in the area of the main stem associated with the lower crown and on the branches of the lower crown. From 26 to 61 percent of the larvae on Douglas-fir were on the main stem.

Mean survival from the egg stage to the feeding stage was 21 percent. Survival during hibernation was 77 percent. Sixteen percent of the hibernating larvae died within their hibernacula.

On a comparé l'exactitude et la facilité d'emploi des méthodes de capture des larves de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) en hibernation sur le douglas taxifolié (*Pseudotsuga menziesii* [Mirb.] Franco). On a étudié le nombre et la répartition des larves sur les branches et les tiges principales du douglas, du mélèze occidental (*Larix occidentalis* Nutt.) et du pin ponderosa (*Pinus ponderosa* Laws.), ce qui a permis de mettre au point des larves sur les tiges, les branches et les rameaux foliés du douglas. On a estimé la survie, du stade de l'oeuf à celui de l'imago, dans deux parcelles du centre-nord de l'État de Washington.

En ayant recours à la lumière, on a retrouvé 88 % des larves qui hibernaient sur les branches des douglas. Le taux obtenu par extraction à la soude caustique et au benzène était de 74 %.

La densité des larves en hibernation était la plus élevée sur la tige, à la hauteur du bas de la cime et sur les branches du bas de la cime. De 26 à 61 % des larves trouvées sur le douglas étaient sur la tige principale.

Le taux moyen de survie, du stade de l'oeuf au stade de l'alimentation, était de 21 %. Durant l'hibernation, il était de 77 %. Seize pour-cent des larves en hibernation sont mortes dans leur hibernaculum.

A Remote Sensing Model to Predict Forest Susceptibility to Budworm Defoliation

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Minimizing effects of western spruce budworm (*Choristoneura occidentalis* Freeman) is an integral part of forest-pest management. Forest managers need to know about potential damage to implement silvicultural techniques that reduce or eliminate stand susceptibility. The models developed during this project use data derived from aerial photographs (1:24 000 nominal scale) and maps to estimate susceptibility. The models can be applied at about $0.05 (U.S.) per hectare ($0.02 per acre).

Models were developed in 1981 using aerial photo and map data to predict defoliation probability for forest stands susceptible to budworm. One such model was modified and used to establish new models appropriate for the Payette National Forest near McCall, Idaho, and the Malheur National Forest near John Day, Oregon. Two different types of models were developed for each area; one predicts amount of defoliation in forest stands, and the other predicts amount of defoliation for individual trees. Elevation (obtained from topographic maps), crown diameter, purity of host type in the stand, and species (obtained from aerial photos) are variables that were consistently correlated with defoliation at the 0.10 significance level. Other variables, like cover type and interactions between variables, were significant in particular models.

Models developed in each test area were applied to the other area but results were poor and suggested that budworm preference changes in different geographical areas. Until data can be collected that explain these geographical differences, the models cannot be applied to any area without testing and, perhaps, recalibration.

Other conclusions were:

- Obtaining percent defoliation from 1:1 700 scale aerial photographs used in this study was difficult and inaccurate.
- For modeling, data on amount of ground-collected defoliation proved more reliable than that taken from aerial photographs.
- A management district of 405 000 ha (1,000,000 acres) could conservatively expect to pay about $0.12 per hectare ($0.05 per acre) for this type of model development.

Predicting amount of defoliation in stands susceptible to budworm defoliation can be done easily and cost effectively using data from resource-scale aerial photography and maps. In areas where these models may not directly apply, new models may be formulated by testing and recalibrating existing models.

La réduction au minimum des dommages causés par la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) fait partie intégrante de la répression des ravageurs forestiers. Les aménagistes ont besoin de connaître les dommages éventuels afin d'exécuter les traitements sylvicoles qui permettront de réduire ou d'éliminer la susceptibilité des peuplements. Les modèles élaborés pendant l'étude s'appuient sur des renseignements tirés de photographies aériennes (échelle nominale de 1/24 000) et de cartes afin d'estimer la susceptibilité. Le coût de revient de l'utilisation des modèles est d'environ 0,05 $ US/ha (0,02 $/acre).

En 1981, on a mis au point des modèles à partir de renseignements tirés de photos aériennes et de cartes afin de prédire les probabilités de défoliation dans les peuplements susceptibles à la tordeuse. Un de ces modèles a été modifié et utilisé pour construire des modèles adaptés à la forêt nationale Payette près de McCall, en Idaho, et à la forêt nationale Malheur près de John Day, en Oregon. Deux types de modèles ont été mis au point pour chaque région: l'un pour prédire l'intensité de la défoliation des peuplements, l'autre l'intensité de la défoliation des arbres. L'altitude (tirée de cartes topographiques), le diamètre de la cime, la proportion de l'hôte type dans le peuplement et l'essence (déterminés à partir des photographies aériennes) sont les variables qui ont été constamment corrélées avec la défoliation, au seuil de confiance de 0,10. D'autres variables, comme le type de couvert et les interactions entre les variables, étaient significatives dans certains modèles.

Chaque modèle mis au point pour une région a été appliqué à l'autre, mais a donné alors des résultats médiocres, ce qui porte à croire que les préférences de la tordeuse varient selon la région. Tant qu'on n'aura pas recueilli de données qui expliquent ces écarts géographiques, les modèles ne pourront servir à aucune autre région sans avoir été vérifiés et peut-être réétalonnés.

Les autres conclusions sont les suivantes:

- La détermination du taux de défoliation, directement à partir des photographies aériennes à l'échelle de 1/1700, a été difficile et a donné des résultats inexacts.
- Pour les besoins de la modélisation, les données recueillies sur place, sur la défoliation, sont plus fiables que les données tirées des photographies aériennes.

— Le type de modélisation présenté, appliqué à un district d'aménagement de 45 000 ha (1 000 000 acres) pourrait revenir à au moins 0,12 $ US/ha (0,05 $/acre).

La prévision de l'intensité de la défoliation dans les peuplements susceptibles à la tordeuse peut se faire facilement et à peu de frais, si on tire les données de photographies aériennes et de cartes qui sont à l'échelle utilisée pour l'étude des ressources. Dans les régions où ces modèles ne peuvent pas être utilisés directement, de nouveaux modèles peuvent être construits par vérification et réétalonnage des modèles existants.

The Geographic Chemoprinting Hypothesis as Applied to Western Spruce Budworm

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The geographic chemoprinting hypothesis "we are where we eat" was evaluated for the western spruce budworm (*Choristoneura occidentalis* Freeman) by discriminant analysis of semiquantitative mineral-profile data generated by energy-dispersive X-ray spectrometry. Adult male and female moths from two stands 1.6 km apart could be clearly distinguished from each other.

Quantitative analysis of 10 elements in foliage of three hosts, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and Engelmann spruce (*Picea engelmannii* Parry) and in rearing medium were compared with elemental concentrations in male and female pupae and adults reared on each of the substrates. Results indicated close homeostatic regulation of most elements, and the variations in concentrations in food materials were not reflected in adult chemical profiles.

A search for non-toxic marker element for the budworm showed that systemic (as compared to foliar) application of rubidium chloride to trees increased the amount of rubidium in new foliage and in budworm feeding on it — and was also transferred to egg masses. The

On a confronté au cas de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) l'hypothèse voulant qu'on puisse déterminer l'origine géographique des insectes grâce à leur composition chimique, laquelle dépend de la nourriture ingérée; on a eu recours à l'analyse discriminante de données semiquantitatives obtenues par spectrométrie par rayons X. Ainsi, les papillons mâles et femelles de deux peuplements distants de 1,6 km pouvaient être clairement distingués les uns des autres.

Les résultats de l'analyse quantitative de 10 éléments présents dans le feuillage de trois essences hôtes, le douglas taxifolié (*Pseudotsuga menziesii* [Mirb.] Franco), le sapin grandissime (*Abies grandis* [Dougl.] Lindl.) et l'épinette d'Engelmann (*Picea engelmannii* Parry), et dans les milieux de culture ont été comparés à ceux qu'on a trouvés dans les chrysalides et les adultes mâles et femelles élevés sur chacun de ces substrats. Les résultats ont montré que la plupart des éléments subissaient une régulation homéostatique et que les variations de concentrations dans les aliments ne se retrouvaient pas dans les profils chimiques des adultes.

marker can be used to study among-tree movement of adult budworm, and egg masses of females from marked trees could be identified on adjacent trees.

La recherche d'un marqueur non toxique a montré que la chlorure de rubidium appliqué de façon endothérapique (plutôt que foliaire) se traduisait par une augmentation de la teneur en rubidium dans le feuillage nouveau et chez les tordeuses qui s'en nourrissaient; par la suite, il se retrouvait dans les masses d'oeufs. Le marqueur peut servir à étudier le déplacement des tordeuses adultes d'un arbre à l'autre, et les masses d'oeufs de femelles provenant d'arbres marqués peuvent être repérées sur des arbres voisins.

Effects on Woodland Ants of the Carbaryl Treatment of the Western Spruce Budworm in Oregon

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In 1983, outbreaks of the western spruce budworm (*Choristoneura occidentalis* Freeman) occurred in the Blue Mountains of eastern Oregon. Aerial application of carbaryl was the primary control tactic. The possible effects of the treatment on the foraging activity of woodland ants were examined, including known predators in the genera *Formica* and *Camponotus*. Pre- and post-treatment samples were collected from ground baits and from drop traps placed under the live crowns of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and true fir (*Abies* spp.) trees. Foraging activity, measured by the number of ants captured per sample, dropped sharply after the spray treatment and remained lower than pre-treatment for at least 6 weeks after the spraying.

En 1983, la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) s'est mise à proliférer dans les Blue Mountains de l'est de l'Oregon. La principale mesure de répression a consisté en traitements aériens au carbaryl. Les effets possibles du traitement sur la recherche de nourriture par les fourmis forestières, y compris des espèces connues des genres *Formica* et *Camponotus*, ont été examinés. Des échantillons de fourmis ont été prélevés, avant et après les traitements, avec des pièges appâtés au sol et d'autres installés sous la couronne vivante de la cime des douglas taxifoliés (*Pseudotsuga menziesii* [Mirb.] Franco) et des sapins (*Abies* spp.). La recherche de nourriture, mesurée par le nombre de fourmis capturées par échantillon, a diminué brusquement après le traitement et est demeurée moins intense qu'avant le traitement, pendant au moins six semaines après ce dernier.

The Relation of Tree Growth Losses to Levels of Defoliation by the Western Spruce Budworm

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The objective of this study was to quantify the effects of western spruce budworm (*Choristoneura occidentalis* Freeman) defoliation on tree growth during and immediately following an infestation. The study provided tree growth/defoliation models for linkage between insect/foliage models and stand growth models. In 1982, 200 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and grand fir (*Abies grandis* (Dougl.) Lindl.) trees were felled from 26 stands in north-central Washington. Expected height and diameter growth without defoliation were predicted using the Stand Prognosis model, and were adjusted for growing season with a model using weather data and soil characteristics. Growth in the preceding year and duration of attack were found to have significant effects on the growth rates when defoliation levels were held constant. Growth effects did not differ between Douglas-fir and grand fir trees when defoliation and attack duration were taken into account. Similarly, tree size, competition level, and growth prior to infestation were not found to affect the amount of growth loss suffered from a given level of defoliation.

L'objet de l'étude était de mesurer les effets de la défoliation causée par la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) sur la croissance à court terme des arbres et la croissance à long terme des peuplements. Dans une première étape, on a établi des modèles portant sur la croissance avec défoliation pour les accoupler à d'autres modèles portant sur les insectes et le feuillage d'une part, et la croissance des peuplements d'autre part. En 1982, 200 douglas taxifoliés (*Pseudotsuga menziesii* [Mirb.] Franco) et sapins grandissimes (*Abies grandis* [Dougl.] Lindl.) ont été abattus dans 26 peuplements du centre-nord de Washington. À l'aide du modèle Prognosis, on a déterminé la croissance prévue en hauteur et en diamètre en l'absence de défoliation et on a ajusté les valeurs pour le temps de croissance à l'aide d'un modèle utilisant des données météorologiques et des caractéristiques pédologiques. On a constaté que la croissance au cours de l'année précédente et la durée de l'attaque par la tordeuse avaient un effet notable sur la vitesse de croissance lorsque l'intensité de la défoliation était maintenue constante. Entre les douglas et les sapins, les effets sur la croissance ne différaient pas lorsque la défoliation et la durée de l'attaque étaient prises en compte. De même, la taille de l'arbre, la compétition et la croissance avant la défoliation n'influaient pas sur la perte de croissance subie par un niveau de défoliation donné.

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How to Protect Individual Trees From Spruce Budworms by Implants and Injections

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Implantation and injection are two methods to protect individual trees from spruce budworms. Implantation is with Medicap®, manufactured by Creative Sales, Inc., Fremont, Nebraska 68025. Medicaps® are tubular plastic cartridges (1 by 2.5 cm) containing a dry chemical encased in a gelatin capsule. The sap dissolves the capsule, and the chemical moves through the tree with the sap. Medicaps® are inconspicuous in use because the implants are driven completely into holes drilled in the trunk of the tree. Medicaps containing concentrated, technical acephate (Orthene®) are called ACECAPS®. These ACECAPS® 97 cartridges, containing 0.9 g of active ingredient, are registered for control of spruce budworms by the Environmental Protection Agency (EPA). They are also approved for use by homeowners.

Injection is with Mauget Systemic Injector Units®, manufactured by J.J. Mauget Company, Burbank, California 91504. No insecticide is currently registered for use with the Mauget injector system® against spruce budworms. Experiments with acephate show the system has promise for controlling budworms, and the Mauget Company has petitioned EPA for registration. Maugets® consist of a body and vial (3 by 4.5 cm) containing liquid chemical that is introduced into the tree trunk through small, plastic feeder tubes.

L'implantation et l'injection sont deux méthodes de protection individuelle des arbres contre les tordeuses. L'implantation utilise les produits Medicaps®, fabriqués par Creative Sales, Inc., de Fremont au Nebraska, 68025. Ce sont des cartouches tubulaires de plastique (1 cm sur 2,5) contenant un produit chimique sec logé dans une gélule. En dissolvant la gélule, la sève entraîne le produit. Leur emploi passe inaperçu car l'implantation se fait dans des trous percés dans le fût de l'arbre. Les Medicaps® contenant de l'acéphate concentré de qualité technique (Orthène®) s'appellent ACECAPS®. Les cartouches ACECAPS® 97, contenant 0,9 g de matière active sont homologuées contre les tordeuses de l'épinette par l'EPA (Environmental Protection Agency). Elles sont aussi approuvées pour usage domestique.

L'injection se fait au moyen d'un injecteur endothérapique Mauget®, fabriqué par J.J. Mauget Company, de Burbank en Californie, 91504. Aucun insecticide n'est actuellement homologué pour utilisation contre les tordeuses au moyen de ce dispositif. Les expériences réalisées avec l'acéphate montrent que la méthode est prometteuse contre les tordeuses, et la compagnie Mauget a demandé à l'EPA de l'homologuer. Le dispositif comprend un corps et une fiole (3 cm sur 4,5) contenant un produit liquide qui est introduit dans le fût au moyen de petits tubes de plastique.

Moth Captures in Pheromone-Baited Traps Relative to Subsequent Defoliation of Douglas-fir by Western Spruce Budworm

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When sticky traps with weak baits are operated without tending through the flight season, the number of male moths caught is highly correlated with severity of defoliation occurring the next year. With baits containing 0.0001 percent pheromone (92:8 blend of E-11 and Z-11 tetradecenal) by weight, average trap catch is more than 95 percent correlated with subsequent defoliation where the moth population is indexed with as few as 9 traps.

Le nombre de papillons mâles capturés dans des pièges collants faiblement appâtés et laissés à eux-mêmes durant la période d'envol est fortement corrélé à la défoliation dans l'année suivante. Avec un appât contenant 0,0001 % de phéromone en masse (mélange de tétradécène — 11E al et de tétradécène — 11Z al, dans une proportion de 92:8), le nombre moyen de captures par piège est corrélé à environ 95 % à la gravité de la défoliation lorsqu'on utilise seulement neuf pièges pour l'indexation des populations.

Defoliation and Douglas-Fir Cone and Seed Losses Caused by Budworm in the Northern U.S. Rocky Mountains

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In September 1979, counts of ovulate buds on 25 randomly selected branchlets on each of 22 Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees at 20 locations in the Northern U.S. Rockies predicted a good cone crop for 1980 throughout the study area. However, potential cone crop was nearly eliminated in areas of moderate to high defoliation by western spruce budworm (*Choristoneura occidentalis* Freeman), especially in Montana east of the Continental Divide and in nearby east-central Idaho. Few cones matured in stands with a 1980 defoliation-rating index greater than 40 percent. Stands with low to moderate defoliation-rating indexes (from 30 to 40 percent) had from 30 to 90 percent of the potential cones killed by budworm larvae. The remaining stands had low defoliation rating indexes (from 2 to 21 percent) and low cone mortality caused by budworm larvae (from 2 to 25 percent of the cone potential). Most of the mortality occurred during the early stages of cone development (92 percent were killed by budworm larvae in the bud or erect conelet stage). These losses accounted for about 80 percent of all seed mortality caused by budworm.

The remaining 20 percent of budworm-caused seed mortality occurred in mature cones. Budworm larvae reduced the number of viable seed in mature cones by 1 to 32 percent, depending on location. Seed loss in live cones increased in areas of greater defoliation. Other insects causing seed losses in mature cones were a cone moth (probably *Barbara colfaxiana* (Kearfott)), a cone worm (probably *Dioryctria* sp.), a scale midge (probably *Contarinia washingtonensis* Johnson), a seed chalcid (probably *Megastigmus spermotrophus* Wachtl), and a seedbug (probably *Leptoglossus occidentalis* Heidemann).

Forest managers should not depend on Douglas-fir cones to provide seed for artificial or natural regeneration when the stand-defoliation index is greater than 30 percent, even in years of potentially heavy cone production. Budworm larvae also decrease seed production in stands with defoliation under 30 percent. To protect Douglas-fir cone crops, insecticide should be applied when the cone and pollen buds open.

En septembre 1979, le dénombrement des bourgeons femelles sur 25 rameaux choisis au hasard sur 22 douglas taxifoliés (*Pseudotsuga menziesii* [Mirb.] Franco) dans 20 stations du nord des Rocheuses, aux États-Unis, a amené à prédire une bonne récolte de cônes pour 1980 dans toute la région étudiée. La récolte prévue a presque été annihilée par la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman), dans les zones de défoliation modérée à élevée, notamment dans le Montana, à l'est de la ligne continentale de partage des eaux, et dans le centre-est voisin de l'Idaho. Peu de cônes sont arrivés à maturité dans les peuplements où, en 1980, l'indice de défoliation était supérieur à 40 %. Dans les peuplements où l'indice était faible à modéré (de 30 à 40 %), de 30 à 90 % des cônes qu'on s'attendait à récolter ont été tués par les larves de tordeuse. Dans les peuplements restants, les indices étaient faibles (de 2 à 21 %) et les larves ont tué peu de cônes (de 2 à 25 % de la possibilité de récolte). La mortalité des cônes est survenue en plus grande partie au cours des premiers stades du développement (92 % dans les stades du bourgeon ou du cônelet dressé). Ces pertes comptaient pour environ 80 % de toute la mortalité des semences provoquée par la tordeuse.

Les 20 % résiduels de mortalité ont touché les cônes à maturité. Les larves ont réduit le nombre de semences viables dans les cônes à maturité de 1 à 32 % selon la localité. Les pertes de semences dans les cônes vivants ont augmenté dans les zones les plus défoliées. Parmi les autres insectes qui ravagent les semences dans les cônes à maturité, citons un perce-cône (probablement *Barbara colfaxiana* [Kearfott]), une pyrale (probablement *Dioryctria* sp.), une cécidomyie (probablement *Contarinia washingtonensis* Johnson), un chalcis granivore (probablement *Megastigmus spermotrophus* Wachtl) et une punaise des semences (probablement *Leptoglossus occidentalis* Heidemann).

Les aménagistes ne devraient pas compter sur les cônes de douglas pour la régénération artificielle ou naturelle, lorsque l'indice de défoliation du peuplement est supérieur à 30 %, même au cours des années où leur production est prometteuse. Les larves de la tordeuse diminuent aussi la production de semences dans les peuplements défoliés à moins de 30 %. Pour protéger les récoltes de cônes de douglas, un traitement insecticide devrait avoir lieu à l'ouverture des bourgeons des cônes et des bourgeons polliniques.

Use of Pheromone-Baited Traps to Evaluate Spruce Budworm Populations

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A spruce budworm (*Choristoneura fumiferana* (Clem.)) monitoring protocol was developed and field tested with pheromone-baited nonsaturating traps. The objective was to apply currently available knowledge and tools to develop a standardized, reliable, and practical technique to monitor sparse to medium-density spruce budworm populations.

Field trials in 1981 (n = 37 five-trap cluster), 1982 (n = 104), and 1983 (n = 84) were undertaken in five Northeastern States and two eastern Canadian provinces.

Covered-funnel traps (CFT) or modified gypsy moth traps (GM plastic canister, GM milk carton) were baited with one of two commercially available lures: Hercon® laminated flake (12 × 12 mm, ave. release rate ca. 272 ng/h of 95:5 E:Z-11-tetradecenal) or Conrel® fiber (ave. release rate ca. 116 and 223 ng/h in 1982 and 1983, respectively, of 96:4 E:Z-11-tetradecenal). Data were analyzed by region (State or province), host (fir or spruce), trap model, and lure type. Mean trap catch was correlated with L_3-L_4 density (within-generation), L_3-L_4 density (between generation), L_2 density, and current defoliation.

Several regional analyses of data from stands that were predominantly fir produced good correlations between mean trap catch and L_3-L_4 (e.g., $r^2 = 0.53$ to 0.96) and L_2 (e.g., $r^2 = 0.73$ to 0.76). However, results of the combined data were variable.

With further improvements in trap design and lure characteristics, forest and pest managers can utilize trap catch to monitor population trend, detect and map large-scale dispersal flights, or determine when populations are high enough to sample with more precise methods. Similarly, trap-catch information may facilitate early decision making relative to other management activities such as timing of egg-mass surveys, identification of potential treatment areas, and adjustment of forest-management plans to accommodate potentially hazardous situations.

Une méthode de surveillance de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) a été mise au point et testée sur le terrain à l'aide de pièges non saturants utilisant des phéromones comme attractifs. Le but était d'appliquer les connaissances et les outils actuels pour mettre au point une technique normalisée, fiable et pratique pour surveiller les populations de tordeuse des bourgeons de l'épinette de densité faible à moyenne.

Des essais sur le terrain en 1981 (n = 37 groupes de 5 pièges), en 1982 (n = 104) et en 1983 (n = 84) ont été entrepris dans cinq États du nord-est des États-Unis et dans deux provinces de l'est du Canada.

Des pièges fermés en forme d'entonnoir et des pièges modifiés pour la spongieuse (flacon de plastique et carton de lait) ont été munis de l'un des deux attractifs suivants disponibles commercialement : paillettes laminées Hercon® (12 × 12 mm, libération moyenne d'environ 272 ng/h de 95/5 des isomères E_{11}/Z_{11} du tétradécènal) et fibres Conrel® (libération moyenne d'environ 116 et 223 ng/h en 1982 et 1983 respectivement de 96/4 des isomères E_{11}/Z_{11} du tétradécènal). Les données ont été analysées par région (État ou province), par essence hôte (sapin ou épinette), par modèle de piège et par genre d'attractif. On a établi une corrélation entre la capture moyenne par piège et la densité L_3-L_4 (dans une même génération), la densité L_3-L_4 (d'une génération à l'autre), la densité L_2 et la défoliation actuelle.

Plusieurs analyses régionales de données provenant de peuplements dominés par le sapin ont produit de bonnes corrélations entre la capture moyenne par piège et L_3-L_4 (par exemple, $r^2 = 0{,}53$ à 0.96) et L_2 (par exemple, $r^2 = 0.73$ à 0,76). Les résultats des données combinées étaient variables.

Grâce à d'autres améliorations dans la conception des pièges et dans les caractéristiques des attractifs, les responsables de la gestion forestière et de la gestion des ravageurs pourront utiliser la capture par piège pour surveiller les tendances de la population, pour détecter et consigner sur une carte les vols de dispersion à grande échelle, ou déterminer à quel moment les populations sont assez grandes pour être échantillonnées avec des méthodes plus précises. De même, l'information obtenue par la capture par piège peut faciliter la prise de décision précoce concernant d'autres activités de gestion comme, par exemple, le moment opportun de procéder à des études des masses d'oeufs, l'identification des zones de traitement potentielles et l'ajustement des projets de gestion forestière pour tenir compte de certaines situations potentiellement dangereuses.

Cutting Methods in a Mixed Aspen/Balsam Fir Stand Affect Spruce Budworm Damage

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When a spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak in northern Wisconsin infested an aspen/balsam fir (*Populus* spp./*Abies balsamea* (L.) Mill.) stand in a cutting study from 1976 through 1980, researchers had the opportunity to observe how the altered stand conditions influenced budworm caused mortality and growth loss. Eight cutting methods had been assigned to five replications in a 36-year-old aspen stand with an understory of 15 to 35 year-old balsam fir in 1950. Measurements in 1981 were compared with the 1975 preoutbreak descriptions. Balsam fir mortality and growth loss were directly related to the level of overstory removal.

Aspen Treatment	Dead Balsam Basal Area %	Growth Loss %
Clearcut at age 36	96	15
Clearcut at age 47	100	20
Commercial clearcut at age 47	98	21
Thin from above at age 36 (2-stick limit)	38	9
Thin from above at age 36 (3-stick limit)	37	4
Thin from above at age 36	35	4
Thin from below at age 39	37	2
Control	30	3

The key to damage was stand composition prior to the budworm outbreak.

Forest managers must weigh the benefits of accelerated balsam fir growth resulting after release from overstory competition by cutting against the potential consequences of a budworm infestation. If presalvage or temporary direct suppression of budworm is feasible, increased yields can result. However, if such a quick response to budworm infestation is in doubt, it may be safer to manage stands as mixtures.

Lorsqu'une pullulation de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) s'est produite dans un peuplement de peuplier (*Populus* spp.) et de sapin baumier (*Abies balsamea* [L.] Mill.) dans le nord du Wisconsin au cours d'une étude de coupe de 1976 à 1980, les chercheurs ont eu l'occasion d'observer comment les conditions modifiées du peuplement influaient sur la mortalité et la perte de croissance dues à la tordeuse. Huit méthodes de coupe ont été pratiquées dans 5 parcelles semblables d'un peuplement de peuplier de 36 ans avec un sous-étage de sapin baumier de 15 à 35 ans en 1950. Les mesures obtenues en 1981 ont été comparées avec celles de 1975, soit avant la pullulation. La mortalité et la perte de croissance du sapin baumier étaient directement reliées à l'ampleur de l'élimination de l'étage supérieur.

Traitement du peuplier	Surface terrière des sapins baumiers morts %	Perte de croissance %
Coupe à blanc à l'âge de 36 ans	96	15
Coupe à blanc à l'âge de 47 ans	100	20
Coupe blanche commerciale à l'âge de 47 ans	98	21
Éclaircie par le haut à l'âge de 36 ans (limite de 2 billes)	38	9
Éclaircie par le haut à l'âge de 36 ans (limite de 3 billes)	37	4
Éclaircie par le haut à l'âge de 36 ans	35	4
Éclaircie par le bas à l'âge de 39 ans	37	2
Témoin	30	3

La clé expliquant les ravages était la composition du peuplement avant la pullulation de la tordeuse.

Les gestionnaires forestiers doivent peser les avantages d'une croissance accélérée du sapin baumier résultant de la coupe destinée à libérer ces derniers de la compétition de l'étage supérieur contre les conséquences potentielles d'une infestation par la tordeuse des bourgeons de l'épinette. Si une coupe de prérécupération ou une suppression temporaire directe de la tordeuse sont faisables, on peut obtenir des rendements accrus. Toutefois, si une réponse aussi rapide à une infestation par la tordeuse est douteuse, il peut être plus sûr de gérer les peuplements comme des peuplements mixtes.

Video Data Base for Salvage Scheduling

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Efficient equipment management is essential to harvest scheduling especially in areas with extensive spruce budworm activity. Dead and dying timber may need almost immediate salvage in order to minimize the loss of potential wood fiber. Central to equipment management is a knowledge of machine productivity. Techniques for equipment study can be costly and time consuming. A system has been developed to manipulate quickly and easily the large volume of data usually produced by conventional time studies. The techniques inherent in this system are particularly advantageous when used on rapidly operating machines such as delimbers and feller bunchers.

The actions of a machine are recorded on video tape, and the cycle times are obtained during playback of the tape. The computer terminal acts as both the stopwatch and the data sheet. The times, along with cycle identification numbers, are automatically stored in the computer. The data are now ready for calculation of elapsed time, statistical analysis, and report generation.

Another aspect of the system involves the measurement of trees from the TV monitor screen. Both length and diameter data can be obtained to provide volumetric criteria to directly associate with cycle times.

The system can be employed to provide logging equipment production/cost relationships to assist in timer salvage scheduling after budworm devastations.

Une gestion efficace de l'équipement est essentielle pour établir le calendrier de récolte, surtout dans les régions présentant une forte activité de la tordeuse des bourgeons de l'épinette. L'instance d'une coupe de récupération des arbres morts et mourants pourrait s'avérer indispensable si l'on veut minimiser les pertes en fibres de bois potentielles. La connaissance de la productivité de la machinerie est primordiale en regard de la gestion de l'équipement. Les techniques utilisées pour l'étude de l'équipement peuvent coûter cher et exiger beaucoup de temps. Un système a été mis au point pour manipuler rapidement et facilement la grande masse de données générées habituellement par les analyses chronométriques traditionnelles. Les techniques inhérentes à ce système sont particulièrement avantageuses pour des machines qui fonctionnent rapidement telles les ébrancheuses et les abatteuses-empileuses.

Les mouvements d'une machine sont enregistrés sur bande vidéo et la durée du cycle est déterminée lors de la lecture de la bande. Le terminal de l'ordinateur agit à la fois comme chronomètre et comme feuille de données. Le temps, ainsi que les chiffres d'identification du cycle, sont automatiquement entrés dans l'ordinateur. Les données sont alors prêtes pour le calcul de la période de temps écoulé, l'analyse statistique et la production de rapports.

Le système permet également d'évaluer la mesure des arbres à partir de l'écran de télévision. Aussi, des données sur la longueur et le diamètre peuvent être obtenues et fournir par le fait même un critère volumétrique que l'on associe directement à la durée du cycle.

Le système peut fournir un rapport production-coût pour l'équipement d'exploitation forestière et permettre à l'établissement d'un calendrier de récupération du bois après une infestation par la tordeuse.

Comparison of Methods for Determining Optimal Sample Size for Spruce Budworm Populations in Newfoundland

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Several methods were evaluated to determine the optimal sample size to estimate early larval (2nd to 4th instars), late larval (5th to 6th instars), pupal, and egg mass density of spruce budworm (*Choristoneura fumiferana* (Clem.)) on balsam fir (*Abies balsamea* (L.) Mill.) branches in Newfoundland for a specified degree of precision and confidence level.

Variance estimates to determine sample size were based on the negative binomial distribution with a common k (Bliss and Owen 1958) and a density-dependent k (Ruesink 1980); regression of mean crowding, $\overset{*}{m}$ as a function of the mean density, m (Iwao and Kuno 1968); and Taylor's Power Law (Taylor 1961). Insect counts for all stages studied could not be described by a common k based on the weighted regression method of Bliss and Owen (1958). Estimates of sample size based on a density-dependent k were found not to differ from those based on Taylor's Power Law and therefore it was concluded that both models were identical but were expressed in different terms. Sample size estimates based on the $\overset{*}{m}$:m regression were about twice as large as those based on Taylor's Power Law. The $\overset{*}{m}$:m model clearly suggested that all stages studied could be described by a common k. Taylor's Power Law, however, provided the most statistically relevant and biologically meaningful variance-mean relationship to estimate optimal sample size. The optimal sample sizes for all stages studied based on this model appear feasible at mean densities greater than or equal to one.

On a évalué plusieurs méthodes avant de déterminer avec un degré de précision et un niveau de fiabilité précis la taille optimale des échantillons nécessaires à l'évaluation de la densité de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]), aux stades larvaires précoces (2^e à 4^e), aux stades larvaires tardifs (5^e et 6^e), au stade de la chrysalide de même qu'au stade de l'oeuf sur les branches de sapin baumier (*Abies balsamea* [L.] Mill.), à Terre-Neuve.

Les estimations de la variance pour déterminer la taille de l'échantillon étaient basées sur la distribution binomiale négative avec un k commun (Bliss et Owen 1958) et un k dépendant de la densité (Ruesink 1980); sur une régression de l'encombrement moyen, $\overset{*}{m}$ comme une fonction de la densité moyenne, m (Iwao et Kuno 1968); sur la loi de puissance de Taylor (Taylor 1961). Les nombres d'insectes à tous les stades de développement utilisés n'ont pu être décrits par un k commun avec la méthode de régression pondérée de Bliss et Owen (1958). On a constaté que les estimations de la taille de l'échantillon, fondées sur un k dépendant de la densité, ne différaient pas des estimations fondées sur la loi de puissance de Taylor; on en a conclu que les deux modèles étaient identiques, mais qu'ils étaient exprimés en termes différents. Les estimations de la taille des échantillons fondées sur la régression $\overset{*}{m}$:m étaient environ deux fois plus grandes que celles fondées sur la loi de puissance de Taylor. Toutefois, le modèle $\overset{*}{m}$:m laissait entendre clairement que tous les stades étudiés pouvaient être décrits par un k commun. Enfin, la loi de puissance de Taylor a fourni les relations variance-moyenne les plus pertinentes du point de vue statistique et les plus significatives du point de vue biologique pour estimer la taille requise des échantillons. Il semble bien, d'après ce modèle, que les tailles optimales d'échantillons pour tous les stades étudiés soient possibles à des densités moyennes égales ou supérieurs à un.

Temperature Controls on Spruce Budworm Moth Emigration — A Geographical Analysis

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Spruce budworm (*Choristoneura fumiferana* (Clem.)) populations expand mainly through dispersal of egg-bearing females. Moths emigrate in significant numbers during 5 to 7 days in July, for about three hours at dusk, and disperse with the wind at heights mostly below 300 m. Exodus flights are suppressed when canopy temperatures drop below 18°C. This leads to 'temperature trapping' in certain geographical locations and imposes limitations on the patterns of large-scale epidemic spread.

The geographical distribution of July early evening temperatures in New Brunswick was determined using mean daily maximum temperature (T_{max}) records from standard climatological stations, adjusted for time and elevation. Time adjustments were based on a study of temperature-decline rates (ΔT) at first-order meteorological stations. Both T_{max} and ΔT were strongly influenced by nearness to the Bay of Fundy and, to a lesser extent, the Gulf of St. Lawrence. The elevation effect was assumed to be -0.8°C/100 m at the time of T_{max}, reducing to about -0.3°C/100 m at the time of maximum moth exodus.

Synoptic weather associations were determined by relating 2000 AST temperatures during July at Fredericton Airport to flow directions measured from the pressure fields on detailed synoptic charts for the period 1958 to 1976. Excluding those occasions when winds were 5 m/s or less, temperatures were favorable for moth exodus on two-thirds of 583 evenings studied. On these occasions, flow directions were from the southwest through west for 84.3 percent of the evenings.

This analysis has considerable significance to the probability of moth influxes from certain sources of abnormal but particular interest — specifically the Gaspé region and eastern Nova Scotia/Cape Breton. The Gaspé sector accounted for only 13 evening flows over 19 years in association with favorable temperatures at Fredericton representing an invasion from the Gaspé into New Brunswick of only one evening every 7.7 years. There were no flows toward New Brunswick from eastern Nova Scotia/Cape Breton with favorable temperatures.

Les populations de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) se propagent principalement par la dissémination des femelles portant des oeufs. Ces femelles émigrent en grand nombre au cours d'une période de 5 à 7 jours en juillet; ce vol a lieu au moment de la brunante et dure environ 3 heures alors que les insectes suivent la direction du vent, généralement à des hauteurs inférieures à 300 m. L'ampleur de ces vols d'émigration est considérablement réduite lorsque les températures sous le couvert forestier tombent au-dessous de 18 °C. De telles conditions viennent confiner les papillons dans certaines régions géographiques, ce qui commande un contrôle à la dissémination à grande échelle.

On a déterminé la répartition géographique des températures en début de soirée durant le mois de juillet, au Nouveau-Brunswick, en utilisant les données sur la température quotidienne maximale (T_{max}) des stations climatologiques conventionnelles, adaptées aux différences de temps et d'élévation. Le réglage en fonction du temps repose sur l'étude des taux de décroissance des températures (ΔT) dans les stations météorologiques de premier ordre. La proximité de la côte de la baie de Fundy et, dans une moindre mesure, du golfe du Saint-Laurent, a influé fortement sur la T_{max} et le ΔT. On a supposé que l'effet dû à l'élévation était de $-0{,}8$ °C/100 m au moment de la T_{max}, et de $-0{,}3$ °C/100 m au paroxisme de l'émigration des papillons.

Les relations de température synoptique ont été déterminées en établissant les relations entre les températures à 2000 HNA en juillet à l'aéroport de Fredericton et les directions d'écoulement de l'air mesurées à partir des champs de pression sur des cartes synoptiques détaillées pour la période de 1958 à 1976, pour un total de 583 cas. À l'exception des cas où les vents étaient de 5 m/s ou moins, les températures étaient favorables à l'émigration des papillons deux soirs sur trois. En de telles occasions les directions d'écoulement de l'air provenaient de sud-ouest en ouest dans 84,3 % des soirs.

Cette analyse est d'une importance considérable du point de vue de la probabilité de l'arrivée des papillons en provenance de sources d'un intérêt particulier, nommément la région de Gaspé et l'est de la Nouvelle-Écosse/Cap-Breton. Le secteur de Gaspé n'est intervenu que pour 13 vols de soirée durant une période de 19 ans, en rapport avec des températures favorables à Fredericton; cela représente, au plus, une invasion du Nouveau-Brunswick en provenance de Gaspé par 7,7

années. Au Nouveau-Brunswick, aucun vol n'a été signalé de l'est de la Nouvelle-Écosse/Cap-Breton lorsque les températures étaient propices à l'émigration.

Ants Preying on Western Spruce Budworm

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The identity of ant species preying on the western spruce budworm (*Choristoneura occidentalis* Freeman) was investigated in eastern Oregon and western Montana in 1981 and 1982. Predation on stocked pupae was observed hourly on trees actively foraged by a range of ant species. The following species were collected as they fed on budworm: *Camponotus laevigatus* (Smith), *C. modoc* Wheeler, *C. vicinus* Mayr, *Formica accreta* Francoeur, *F. lasioides* Emery, *F. neorufibarbis* Emery, *F. obscuripes* Forel, *F. podzolica* Francoeur, and *F.* sp. (*microgyna* group). The *Camponotus* species and *F. obscuripes* comprised 85 percent of all ants preying on pupae.

The distribution of ant predators was studied in 1982 on 24 sites in eastern Oregon and 24 sites in western Montana. Sites were selected along a moisture-temperature gradient indexed by vegetational composition (habitat type). Ant density and species composition were determined by trapping foraging ants on randomly selected trees. Several site and stand variables were correlated with ant abundance by species.

Nine species of *Formica* and *Camponotus* were collected in Montana and 11 species in Oregon. Four species were common in both States — *C. modoc, C. vicinus, F. neorufibarbis*, and *F. podzolica*. *Camponotus herculeanus* (L.) was common in Montana. Changes in ant species composition and abundance along the moisture-temperature gradient were pronounced. Fewer ants or ant species were collected in the warm–dry habitat types or in the cold–wet habitat types. The species distribution varied between States, and their abundance was correlated with a different set of environmental variables. Across almost all habitat types, each common species was more abundant in stands where average canopy coverage was less than 90 percent.

En 1981 et 1982, on a identifié les fourmis prédatrices de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman), dans l'est de l'Oregon et l'ouest du Montana. On a observé horairement la prédation d'amas de chrysalides deposés dans les arbres prospectés activement par une gamme d'espèces de fourmis. Les suivantes ont été prises sur le fait: *Camponotus laevigatus* (Smith), *C. modoc* Wheeler, *C. vicinus*, Mayr, *Formica accreta* Francoeur, *F. lasioides* Emery, *F. neorufibarbis* Emery, *F. obscuripes* Forel, *F. podzolica* Francoeur, *F.* sp. (groupe des *microgyna*). Les *Camponotus* et *F. obscuripes* comprenaient 85 % de toutes les fourmis capturées.

La répartition des fourmis prédatrices a été étudiée en 1982, dans 24 stations de chacune des deux régions susmentionnées. Les stations ont été choisies selon leur emplacement le long d'un gradient d'humidité et de température indexé selon la composition floristique (type d'habitat). La densité des fourmis et la composition des espèces ont été déterminées par captures des fourmis à la recherche de nourriture sur des arbres choisis au hasard. Plusieurs variables stationnelles et de peuplement ont été corrélées avec l'abondance des fourmis de chaque espèce.

Neuf espèces de *Formica* et de *Camponotus* ont été capturées au Montana, 11 en Oregon. Quatre étaient communes dans les deux États: *C. modoc, C. vicinus, F. neorufibarbis* et *F. podzolica*. *C. herculeanus* (L.) était répandu au Montana. Les variations de la composition des espèces et de leur abondance le long du gradient étaient prononcées. Peu de fourmis ou d'espèces de fourmis ont été capturées dans les habitats chauds et secs ou dans les habitats froids et humides. La répartition des espèces variait entre les États, et leur abondance était corrélée à un ensemble différent de variables mésologiques. Dans la plupart des types d'habitats, chaque espèce commune abondait davantage dans les peuplements où le couvert était inférieur à 90 %.

Preventing Western Spruce Budworm Damage with Silvicultural Cuttings

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Silvicultural cuttings to regulate species composition, stand density, stand size-class structure, tree vigor, and stand maturity can reduce or prevent damage by western spruce budworm (*Choristoneura occidentalis* Freeman) if properly designed and implemented. Knowledge of the budworm's habitat requirements and behavior, along with an understanding of how stands respond to defoliation, allow us to define conditions in highly susceptible and vulnerable stands. Cutting prescriptions can then be designed to create and maintain stand conditions that are less susceptible to infestation and less vulnerable to damage.

Western spruce budworm infestations are typically associated with climax or near climax stands on relatively dry sites. High-hazard stands are generally pure shade-tolerant hosts, highly dense, uneven-aged, low in tree vigor, and of advanced age. Subclimax stands of seral host trees on mesic sites can also be infested, but less frequently and only when close to high-hazard stands or during periods of abnormal moisture stress. Sanitation cutting for western spruce budworm usually creates seral, even-aged, vigorous stands of mixed host and nonhost. On some mesic sites, cuttings could promote succession to nonhost. Either way, the target stand should be tailored to the susceptibility of the site and of surrounding stands. Wholesale discrimination against all host species is not required, but regulating the stocking of climax host trees is important.

Clearcut, seed-tree, and shelterwood reproduction cuttings can be particularly effective in producing the seral even-aged stands that are poor habitat for budworm. Host seed-trees become a liability to host regeneration and should be removed as soon as regeneration becomes established. Uneven-aged methods have limited use, but could be effective on low-hazard sites or where nonhost trees are climax. Release cuttings can further regulate species composition and vulnerability by removing subordinate crown classes and increasing vigor of the residual stand. Selection thinnings are often harmful. Demonstrations have been established to monitor the response of budworm and its hosts to various cutting methods.

Because western spruce budworm infestations are associated with relatively unproductive climax forest communities, sanitation recommendations appear to be compatible with maximum timber production. For the stands that are properly treated, protection benefits accrue immediately and only gradually attenuate with time as the resulting forest community naturally be-

Grâce à différents régimes sylvicoles bien conçus et bien appliqués pour maîtriser la composition des essences, la densité des peuplements, la structure des classes de grosseur dans les peuplements, la vigueur des arbres et la maturité des peuplements, on peut réduire ou prévenir les dommages causés par la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman). La connaissance des exigences de la tordeuse et de son comportement de même que des réactions des peuplements à la défoliation permet de préciser les conditions dans les peuplements très vulnérables aux dommages et très exposés aux infestations. On peut alors prescrire des régimes visant à créer ou à maintenir des conditions qui protégeront les peuplements contre les infestations et les dommages.

Les infestations de la tordeuse occidentale de l'épinette se déclarent habituellement dans les peuplements climaciques ou près de l'être, en stations relativement sèches. Les peuplements les plus menacés sont généralement constitués à 100 % d'hôtes tolérant l'ombre, ils sont très denses, inéquiennes, les arbres manquent de vigueur et sont âgés. Les peuplements au stade sérial du subclimax sont constitués d'arbres hôtes qui, dans les stations mésiques, peuvent aussi être infestés, mais moins souvent et seulement lorsqu'ils sont près de peuplements très menacés, au cours de périodes de sécheresse anormale. La coupe sanitaire antitordeuse crée habituellement des peuplements sériaux mélangés d'arbres hôtes et non hôtes, vigoureux, équiennes. D'une façon ou d'une autre, le peuplement cible devrait être traité selon la susceptibilité de la station et les peuplements qui l'entourent. Il n'est pas nécessaire de discriminer à tout prix contre toutes les essences hôtes, mais il importe de faire la régulation des arbres hôtes au stade climacique.

La coupe à blanc, les arbres semenciers et le mode de reproduction par coupe progressive peuvent être particulièrement efficaces pour l'obtention de peuplements équiennes et sériaux qui sont des habitats défavorables pour la tordeuse. Les semenciers hôtes deviennent un poids mort pour la régénération des hôtes et devraient être éliminés dès que la régénération est implantée. Les méthodes qui favorisent les peuplements inéquiennes sont d'un emploi limité, mais pourraient être efficaces dans les stations peu menacées ou celles où les arbres non hôtes ont atteint le climax. Les coupes de dégagement peuvent assurer la maîtrise de la composition des essences et favoriser une croissance vigoureuse. Les éclaircies peuvent

comes more susceptible. Ordered treatment of highly susceptible stands provides some degree of protection to untreated stands and eventually could result in the prevention of widespread outbreaks. During infestations, directing silvicultural cuttings to the stands most vulnerable to economic loss is the wisest course.

réduire la susceptibilité et la vulnérabilité, grâce à l'élimination des classes de cimes non dominantes et à l'accroissement de la vigueur des arbres résiduels. L'éclaircie jardinatoire cause souvent des dommages. On a expérimenté sur place la réaction de la tordeuse et de ses hôtes à divers régimes.

Comme les infestations de la tordeuse occidentale de l'épinette touchent les communautés forestières climaciques et relativement improductives, les coupes sanitaires recommandées semblent compatibles avec une production maximale de bois. Dans les peuplements bien traités, les avantages de la protection se font sentir immédiatement et ne s'atténuent que graduellement avec le temps, à mesure que la communauté forestière devient naturellement plus susceptible. Le traitement avisé des peuplements très susceptibles procure un certain degré de protection et pourrait aboutir à la prévention des infestations à grande échelle. Au cours des infestations, l'applications des régimes sylvicoles aux peuplements les plus vulnérables aux pertes économiques est la solution la plus sage.

Reducing Douglas-Fir Seed and Cone Damage

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During 1979 and 1980, single, double, and triple ground-applications of acephate and carbaryl were used to improve Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seed and cone production in areas of moderate to heavy western spruce budworm (*Choristoneura occidentalis* Freeman) populations. Ten single-tree replications were used for all treatments. Cone-bearing Douglas-fir trees 9 to 18 m (30 to 60 ft.) tall were selected by examining cone buds, then randomly assigned one of the three treatments. Mixing and application rates were according to label instructions: acephate — 400 g (300 g AI) in 500 L water (⅔ lb. [½ lb. AI] in 100 gal. water); and carbaryl — 2.5 L (1.2 kg AI) in 500 L water (2 qt. [2 lb. AI] in 100 gal. water).

Each tree was sprayed beyond the point of runoff with a hydraulic pumper and handgun operated at 28 kg/cm^2 (400 lb./in.^{2}). The single application, timed to coincide with peak second instar spring dispersal, was

En 1979 et 1980, des traitements uniques, doubles et triples d'acéphate et de carbaryl, à partir du sol, ont servi à améliorer la production de semences et de cônes de douglas taxifolié (*Pseudotsuga menziesii* [Mirb.] Franco) dans les régions où les populations de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) étaient moyennes à élevées. Les trois traitements, répétés 10 fois, ont été appliqués à des arbres isolés. Après examen des bourgeons reproducteurs, on a choisi des douglas de 9 à 18 m (30 à 60 pi) de hauteur porteurs de cônes, puis on leur a donné au hasard l'un des trois traitements. Chaque insecticide a été mélangé et appliqué conformément aux instructions de l'étiquette: acéphate, 400 g (300 g d'ingrédient actif [IA]) dans 500 L d'eau (⅔ lb [½ lb d'IA] dans 100 gal US d'eau); carbaryl, 2,5 L (1,2 kg d'IA) dans 500 L d'eau (2 pintes US [2 lb d'IA] dans 100 gal US d'eau).

on May 21, 1979, when cone buds had expanded to 2.54 cm (1 in.) long and were still erect. Post-spray densities of fourth instars for acephate, carbaryl, and control were 3,6. 1.3, and 21.2 larvae per 100 shoots, respectively; defoliations after pupation were 10.8, 2.2, and 73.0 percent, respectively. Of the potential 68 seeds per cone, the single application provided seed production per cone of 0.5 seed for acephate, 1.0 seed for carbaryl, and no seeds for control. These less-than-expected results were primarily because budworm feeding had damaged over 30 percent of the cones before treatment and because subsequent cone damage by budworm and other seed-and-cone species had caused additional damage before cone harvest on August 23. To reduce pre-spray infestation losses and provide longer protection, double and triple applications were tested the next year. The first applications were on May 8 and 9, 1980, coinciding with the beginning of larval dispersal, which peaked on May 24. This earlier timing reduced pre-spray cone damage to less than 14 percent. The second applications were on May 27 and 28. The last of the triple application was on June 16. Post-spray, mature budworm larvae per 100 shots for acephate, carbaryl, and control were 0.9, 0.6, and 16.3 for double application and 0.3, 0.0, and 16.3 for triple application; defoliation was 4.8, 0.9, and 77.5 percent for double application and 1.3, 0.6, and 77.5 percent for triple application. Mature cones were collected on August 18. Total seed yield for acephate, carbaryl, and control were 34.2, 41.4, and 22.5. Total seed yield for all spray treatments were significantly different from the control, but no significant differences were found between acephate and carbaryl or between double or triple applications. Seed condition (sound, hollow, and insect-damaged) and germination differences were small, variable, and not related to treatment. Where seed yields are important and budworm populations are moderate to heavy, a double application of either acephate or carbaryl is recommended. Time the first application when budworm larvae first begin spring dispersal, and follow with a second in about 14 days.

Le traitement de chaque arbre a duré jusqu'au point de ruissellement. On s'est servi d'une pompe hydraulique et d'un pistolet fonctionnant à 28 kg/cm^2 (400 lb/po^2). Le traitement unique, dont le moment avait été choisi pour coïncider avec le maximum de la dispersion printanière au second stade, a eu lieu le 21 mai 1979, alors que les bourgeons reproducteurs mesuraient environ 2,54 cm (1 po) de longueur et étaient encore dressés. La densité des larves du quatrième stade, après le traitement à l'acéphate, au carbaryl et dans les arbres témoins, était respectivement de 3,6, 1,3 et 21,2 par 100 pousses; la défoliation après chrysalidation était respectivement de 10,8, de 2,2 et de 73,0 %. Au moment du traitement unique, il y avait possibilité de 68 semences par cône et la production par cône a été de 0,5 pour l'acéphate, 1,0 pour le carbaryl et nulle chez les témoins. Ces résultats décevants s'expliquent surtout parce que la tordeuse avait déjà endommagé plus de 30 % des cônes avant le traitement et parce que les dommages subséquents, y compris ceux d'autres espèces de ravageurs des cônes et des semences, s'y sont ajoutés avant la récolte du 23 août. Afin de réduire les dégâts hâtifs et de procurer une protection plus durable, on a expérimenté l'année suivante des traitements doubles et triples. Les premiers traitements ont eu lieu les 8 et 9 mai 1980, coïncidant avec le début de la dispersion des larves, laquelle a atteint son maximum le 24 mai. Ce traitement préventif a réduit les dommages hâtifs aux cônes à moins de 14 %. Le deuxième traitement a eu lieu les 27 et 28 mai, et le troisième, le 16 juin. Dans le cas du double traitement, le nombre de larves à maturité sur 100 pousses était respectivement de 0,9, 0,6 et 16,3 pour l'acéphate, le carbaryl et les témoins. Dans le cas du traitement triple, les chiffres étaient 0,3, 0,0 et 16,3, respectivement. Quant à la défoliation, elle était respectivement de 4,8, 0,9 et 77,5 %. pour le double traitement; et de 1,3, 0,6 et 77,5 % pour le triple traitement. Les cônes mûrs ont été cueillis le 18 août. Le rendement total en semences, à la suite des traitements à l'acéphate, au carbaryl et chez les témoins, était de 34,2, 41,4 et 22,5 respectivement. Dans tous les cas où il y avait eu traitement, le rendement était significativement différent de celui des témoins, mais aucune différence significative n'a été observée entre les résultats du traitement à l'acéphate et au carbaryl ou entre les traitements doubles et triples. L'état des graines (en bon état, vides ou endommagées par les insectes) et le taux de germination différaient peu, tout en étant variables, et n'étaient pas corrélés aux traitements. Lorsque les rendements en semences sont importants et que les populations de tordeuses sont moyennes à élevées, un double traitement à l'acéphate ou au carbaryl est recommandé. Le premier devrait avoir lieu lorsque les larves de la tordeuse entreprennent leur dispersion printanière; le second, 14 jours plus tard.

Effect of the Spruce Budworm on Growth and Survival of Semi-mature Balsam Fir in Newfoundland

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The recent outbreak of the spruce budworm (*Choristoneura fumiferana* (Clem.)) in Newfoundland lasted from 1972 to 1984. Mortality of balsam fir (*Abies balsamea* (L.) Mill.) began in 1976 and is still continuing. The total volume of fir stands with tree mortality was over 40 000 000 m^3 in 1983. The effect of the outbreak was substantial with a major decrease in the current forest inventory. Trees in all crown classes died but mortality was proportionally greater in the intermediate and suppressed crown classes. Stand density and site quality had only slight influence on the number and proportion of trees damaged, but stand age had a consistent effect. Mortality increased with stand age up to 80 to 200 years but decreased above that age. Preliminary estimates of growth loss in surviving trees in severely damaged stands varied widely. Armillaria root rot caused by *Armillaria mellea* (Vahl ex Fr.) Kummer was common in trees of all degrees of cumulative budworm damage but its precise role in the death of damaged trees was not determined. Hardwood moose browse in semi-mature stands increased with budworm damage. In immature stands moose browse decreased initially but increased rapidly caused by an increase in hardwood browse and recovery of softwood trees.

La dernière pullulation de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) à Terre-Neuve a duré de 1972 à 1984. Depuis 1976 jusqu'à maintenant, on enregistre des cas de mortalité chez les sapins baumiers (*Abies balsamea* [L.] Mill.). En 1983, le volume total de peuplements de sapins comptant des arbres morts dépassait 40 millions de mètres cubes. Cette pullulation a eu de graves conséquences, réduisant de façon importante l'inventaire forestier. Des arbres ont été atteints mortellement dans toutes les classes de cime, mais la mortalité a été proportionnellement plus élevée dans les classes intermédiaire et dominée. La densité du peuplement et la qualité stationnelle n'ont eu qu'une influence mineure sur le nombre et la proportion d'arbres endommagés, mais l'âge du peuplement a été un facteur constant. On a observé que le pourcentage de mortalité augmentait avec l'âge du peuplement jusqu'à 80 à 200 ans, puis diminuait. Les estimations préliminaires de la perte de croissance chez les arbres survivants dans des peuplements sévèrement endommagés variaient énormément. Le pourridié-agaric à *Armillaria mellea* (Vahl ex Fr.) Kummer était fréquent chez les arbres pour tous les degrés de dommages cumulatifs causés par la tordeuse, mais son rôle précis dans la mort des arbres endommagés n'a pas été déterminé. Dans les peuplements semi-matures et matures, le broutement des feuillus par les orignaux augmentait en fonction des dommages causés par la tordeuse. Dans les peuplements non matures, le broutement diminuait au début, puis augmentait rapidement suite à l'augmentation des broutilles de feuillus et au rétablissement des résineux.

Road Classification for Wood Flow Strategies

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The increasing costs of timber transportation and road construction, together with the increasing need for more information to support forest management, make it necessary to have detailed forest road and structure data available for maintenance scheduling, route optimization, travel-time estimation, road inventory, and new road location. The establishment of wood-flow patterns is particularly crucial to the harvest scheduling of timber damaged by spruce budworm (*Choristoneura fumiferana* (Clem.)). Road networks, their quality and quantity, are fundamental to any deliberations on wood flow. The structures included in this study are culverts, bridges, gates, and obstacles. A map-based information system that combines computer graphics and data-base technology offers the user the advantages of both the subsystems. The identification of road and structure characteristics, the examination of the possibility to quantify and/or qualify these parameters, the development of a data-base model, and the collection of sample data base by generating basic reports and maps are described.

En raison des coûts croissants du transport du bois et de la construction des routes, et compte tenu du besoin croissant d'information dans la gestion forestière, il est nécessaire d'avoir des données détaillées sur les routes forestières et leurs structures afin de préparer les calendriers d'entretien, d'optimiser les trajets, d'estimer la durée du transport, de faire l'inventaire des routes et de déterminer l'emplacement des nouvelles routes. L'établissement d'un plan d'acheminement du bois est particulièrement important lorsqu'on veut planifier la récolte du bois endommagé par la tordeuse (*Choristoneura fumiferana* [Clem.]). La connaissance des réseaux routiers, tant du point de vue de la qualité que de la quantité, est fondamentale dans le choix d'un plan d'acheminement du bois. Cette étude comprend des structures comme les ponceaux, les ponts, les barrières et les obstacles. Un système d'information cartographique qui combine la technologie de l'infographie et de la banque de données offre à l'utilisateur les avantages des deux sous-systèmes. Cette étude traite des caractéristiques et structures des routes, de la possibilité de quantifier ou de qualifier ces paramètres, de la mise au point d'un modèle de banque de données et du prélèvement de données par la production de rapports et de cartes de base.

Spruce Budworm Characteristics and Foliar Nutrient – Site Relationships in Black Spruce

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Relationships between spruce budworm (*Choristoneura fumiferana* (Clem.)) characteristics and site influences including foliar organic and inorganic nutrient levels, soils, and silvicultural treatments were investigated in a young (ca. 25-year old) black spruce (*Picea mariana*

Dans un jeune peuplement (d'environ 25 ans) d'épinette noire (*Picea mariana* [Mill.] B.S.P.) du nord du Maine, nous avons étudié les relations entre les caractéristiques de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) et l'influence de la

(Mill.) B.S.P.) stand in northern Maine. The influence of foliar N, P, K, Ca, Mg, phenols, flavanoids, and sugars; soil N, P, K, Ca, and Mg; and silvicultural treatments of fertilization, drainage, thinning, and slash removal on budworm population, pupae size, and sex ratio were examined. Silvicultural treatments which enhanced site productivity were positively correlated with pupal population and sex ratio and negatively correlated with female pupae weight and width. Foliar sugars were positively correlated with pupae weight and width and negatively with population. Linear models were constructed relating budworm variables with measured stand, foliar, and soil variables.

station, y compris le sol, les traitements sylvicoles et la teneur en matières nutritives organiques et minérales des aiguilles. Nous avons examiné l'influence de N, P, K, Ca, Mg, des phénols, des flavonoïdes et des sucres foliaires; de N, P, K, Ca et Mg du sol; des amendements, du drainage, des coupes d'éclaircie et de l'enlèvement des rémanents sur les effectifs, la grosseur des chrysalides et le sex-ratio des tordeuses. Il y avait une corrélation positive entre les traitements sylvicoles qui augmentaient la productivité des stations et les effectifs et le sex-ratio des chrysalides; la corrélation était négative entre ces mêmes traitements et le poids et la largeur des chrysalides femelles. Entre les sucres foliaires et le poids et la largeur des chrysalides, la corrélation était positive; négative entre les sucres et les effectifs. Nous avons construit des modèles linéaires des relations entre les variables relatives à la tordeuse et les variables mesurées relatives à la station, aux aiguilles et au sol.

What is Technology Transfer?

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Technology transfer is a concept that is frequently misunderstood. Commonly, it is defined as the purposeful diffusion of an innovation. It is more than this. Technology transfer is a holistic process that involves research, development, commercialization, and diffusion of an innovation, culminating with the consequences of the diffusion. The actual transfer on an innovation is only part of this larger process. It includes an individual decision making process through which a person passes from first knowledge of an innovation, to a decision to adopt or reject, to an implementation of the innovation, to a confirmation of that decision. It is this holistic perspective of technology transfer that has served as the basis of design, implementation, and evaluation of the Spruce Budworm Technology Transfer Program for the Lake States region.

Le transfert de technologie est un concept qui est souvent mal compris. De façon courante, on le définit comme la diffusion intentionnelle d'une innovation technologique. Mais il y a plus encore. Le transfert de technologie est un processus global qui fait intervenir la recherche, le développement, la commercialisation et la diffusion d'une nouveauté, et qui culmine avec les conséquences de cette diffusion. Le transfert proprement dit de l'innovation n'est qu'une partie de ce processus beaucoup plus vaste. Il suppose une prise de décision individuelle qui amène la personne à suivre tout un cheminement: premier contact avec le produit, décision d'adopter ou de rejeter, mise en application de la nouveauté, confirmation de cette décision. C'est cette perspective globale du transfert de technologie qui a servi de base à la conception, la mise en application et l'évaluation du programme de transfert de technologie relatif à la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) pour la région des États des Grands lacs.

Economic Impact of the Spruce Budworm Outbreak in Newfoundland

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The forest resource and dependent industries are a major source of employment and income in Newfoundland. The current spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak has caused serious damage to balsam fir (*Abies balsamea* (L.) Mill.) stands resulting in possible softwood deficits in the next decade. The recent appearance of black spruce (*Picea mariana* (Mill.) B.S.P.) mortality further compounds problems of ensuring adequate future softwood supplies. Shortfalls in the softwood annual allowable cut will impact mostly on the pulp and paper industry. For example, a 20 percent reduction in industrial activity could result in the loss of 980 jobs, annual incomes of $21 million, and value added of $50 million. Further output reductions could possibly lead to mill closures. These losses would have serious economic and social implications for Newfoundland.

Les ressources forestières et les industries qui en dépendent constituent une source importante d'emploi et de revenus pour l'économie de Terre-Neuve. La pullulation actuelle de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) a causé de sérieux ravages dans les peuplements de sapin baumier (*Abies balsamea* [L.] Mill.), si bien qu'on prévoit une pénurie de bois de conifères au cours de la prochaine décennie. L'apparition récente de la mortalité de l'épinette noire (*Picea mariana* [Mill.] B.S.P.) rendra encore plus difficile un approvisionnement suffisant en bois de conifères dans l'avenir. Le fait de ne pas pouvoir réaliser la coupe annuelle permissible en conifères touchera surtout l'industrie des pâtes et papiers. Par exemple, les pertes résultant d'une réduction de l'activité industrielle de 20 % pourraient s'élever à 980 emplois, à 21 millions de dollars en revenus annuels et à 50 millions de dollars en d'autres valeurs. D'autres réductions de la récolte pourraient même entraîner la fermeture d'usines. De telles pertes auraient des conséquences économiques et sociables très sérieuses pour la province.

Nitrogen as an Indicator of Foliage Quality to the Spruce Budworm

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It has been hypothesized that population fluctuations of foliage eating insects are a result of changes in food quality. The level of nitrogen and chemicals in foliage influencing nitrogen utilization are often cited as factors that determine the nutritional quality of foliage. Spruce budworm (*Choristoneura fumiferana* (Clem.) outbreaks have been associated with host species, host maturity, site condition, and weather induced tree stress.

Our studies examined the effect on pupal weight of foliar nitrogen, sugars, phenolics, and tannins in four

On a émis une l'hypothèse selon laquelle les fluctuations des populations d'insectes phyllophages résultent de changements dans la qualité relative de leur alimentation. Le niveau d'azote et de produits chimiques du feuillage, qui influent sur l'utilisation de l'azote, sont souvent cités comme des facteurs qui déterminent la qualité nutritive des feuilles. Les pullulations de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) ont été corrélées avec les essences hôtes, à la maturité de l'hôte, à l'état du site et au stress des arbres provoqué par le climat.

host species, in three age classes, in wet or dry sites, and in silviculturally treated areas (drained, thinned, fertilized). The only factor showing a consistent correlation with pupal weight was nitrogen. Pupae from larvae eating foliage with a higher percentage of nitrogen, were larger. Food conversion studies also indicated that the level of foliar nitrogen is more critical than factors that may affect nitrogen utilization efficiency. Although these studies were limited, it does seem that foliar nitrogen levels offer promise as an indicator of host plant suitability.

Nous avons examiné l'effet de l'azote, des sucres, des phénols et des tannins des feuilles de quatre essences hôtes, appartenant à trois classes d'âges, dans des sites humide ou sec et dans des régions ayant subi des traitements sylvicoles (drainage, éclaircie, fertilisation) sur le poids des chrysalides. Le seul facteur qui a présenté une corrélation constante avec le poids des chrysalides était l'azote. Les chrysalides provenant de larves ayant consommé des feuilles avec un pourcentage d'azote plus élevé étaient plus grosses. Les études de conversion alimentaire ont également indiqué que la teneur des feuilles en azote était plus importante que les facteurs qui déterminent l'efficacité de l'utilisation de l'azote. Bien que ces études aient une portée limitée, il semble que la teneur des feuilles en azote soit un indicateur prometteur pour déterminer la vulnérabilité de la plante hôte.

Information Packages from the Spruce Budworm Technology Transfer Program for the Lake States Region

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Developing and packaging materials was an integral component of our technology transfer program. Our choice of what information to package was based on needs-assessment surveys, the expertise of our staff, products transferred or expected to be transferred by others, and the utility and practicality of the subject matter. We often used the advertising marketing technique of providing several different kinds of media to get a message across.

For example, a general manual on all aspects of spruce budworm, (*Choristoneura fumiferana* (Clem.)) biology and spruce-fir management was supplemented with cassette tapes, computer packages, articles in popular and technical magazines, and slide-tape programs. A remote sensing manual was accompanied by workshops. A silviculture handbook was followed by a videotape to visually summarize and document current approaches to spruce-fir management. A handbook on insecticides was followed by a one-page leaflet to give forest managers basic information more quickly. We used newspaper releases and radio and television spots and interviews to reach private landowners who do not possess technical training in forest

La mise au point et la présentation du matériel faisaient partie intégrante de notre programme de transfert de technologie. Le choix de l'information à présenter a été fondé sur les enquêtes d'évaluation des besoins, sur les connaissances du personnel, sur les produits faisant l'objet du transfert ou pour lesquels on prévoyait un transfert par d'autres, et sur l'utilité et le caractère pratique du sujet traité. Nous avons souvent utilisé des techniques de mise en marché et eu recours à plusieurs types de médias pour faire passer le message.

Par exemple, une publication générale sur tous les aspects de la biologie de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) et l'aménagement de l'épinette et du sapin a été accompagnée par des cassettes, des logiciels, des articles de revues populaires et techniques et des diaporamas. Un manuel de télédétection a été accompagné d'ateliers. Un manuel de sylviculture a été suivi d'une bande vidéo pour résumer visuellement et documenter les approches actuelles dans l'aménagement de l'épinette et du sapin. Un manuel sur les insecticides a été suivi d'un feuillet pour communiquer plus rapidement l'information de base aux gestionnaires forestiers. Nous

management and rarely seek information through traditional forester-oriented agencies. Poster displays were used to advertise the technology transfer program and to make the general public and foresters aware that spruce budworm information was available and where they could obtain it.

avons utilisé des communiqués de presse ainsi que des messages publicitaires et des entrevues à la radio et à la télévision pour atteindre les propriétaires privés qui n'ont pas la formation technique en gestion forestière et qui s'adressent rarement aux organismes en place dans le domaine forestier pour obtenir de l'information. Des affiches ont été utilisées pour faire connaître le programme de transfert de technologie et pour signaler au grand public et aux forestiers qu'il existe de l'information sur la tordeuse des bourgeons de l'épinette et leur indiquer où on peut l'obtenir.

How to Make Technology Transfer Work for You

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The Spruce Budworm Technology Transfer Program for the Lake States Region operated under a flexible plan where activities and procedures were continually evaluated and refined. Unlike agriculture, forestry has had few well organized or time-tested technology transfer programs. For this reason, we feel obligated to document our approach and to describe the factors that impeded or promoted the success of this technology transfer program in forest pest management. There are at least 15 factors that should be considered when developing such a program.

Le programme de transfert de technologie relatif à la tordeuse des bourgeons de l'épinette pour la région des États des Grands lacs a été réalisé dans un cadre flexible où les activités et les méthodes étaient continuellement ré évaluées et perfectionnées. Contrairement à l'agriculture, la foresterie a connu très peu de programmes de transfert de technologie qui étaient bien structurés ou qui avaient été mis à l'épreuve du temps. Pour cette raison, nous avons jugé bon d'étayer notre approche et de décrire les facteurs qui entravaient ou favorisaient ce programme dans le domaine de la gestion des ravageurs forestiers. Il y a au moins 15 facteurs dont il faut tenir compter lorsqu'on veut mettre au point un tel programme.

Biological Impact of the Spruce Budworm in Michigan's Upper Peninsula

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The Michigan Impact Plot System (MIPS) was established during 1978-79 to measure the impact of the

Le *Michigan Impact Plot System* (MIPS) a été mis en place durant l'année 1978-1979 pour mesurer l'inci-

spruce budworm (*Choristoneura fumiferana* (Clem.)) in the Ottawa and Hiawatha National Forests. The 136 ground sampling units in the MIPS were evaluated once each year from 1978 through 1984. Impact data by district and National Forest are presented for the following parameters: percentage of balsam fir (*Abies balsamea* (L.) Mill.) mortality, total dead volume by host species, dead basal area of host species, and live basal area of host species. Approximately twice as much mortality occurred on balsam fir as on white spruce (*Picea glauca* (Moench) Voss) or black spruce (*Picea mariana* (Mill.) B.S.P.) in both National Forests. Balsam fir mortality has been extremely variable in the Hiawatha National Forest. Balsam fir tree mortality in mature stands is very high in the eastern districts (74 to 90 percent), while fir maturity is still under 25 percent in each of the three western districts. These extreme differences in percentage of mortality are due primarily to the good markets for spruce and fir pulp in the western districts. There was little opportunity to harvest fir timber in the eastern districts due to lack of markets. Fir mortality in the Ottawa National Forest ranged by district from 19 to 54 percent through 1983. By 1983, the estimated total dead volume of balsam fir had reached over 486 000 and 583 000 m^3 (17 and 20 million ft^3) in the Hiawatha and Ottawa National Forests. Approximately 90 and 84 percent of the total dead volume is fir. A 36 and 30 percent reduction in live basal area of balsam fir was found in the Hiawatha and Ottawa National Forests, respectively, during the last 5 years.

dence de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) dans les forêts nationales d'Ottawa et d'Hiawatha. Les 136 unités d'échantillonnage au sol faisant partie du MIPS ont été évaluées une fois par année de 1978 jusqu'à 1984. Les données sur l'incidence en fonction du district et de la forêt nationale sont présentées dans le cas des paramètres suivants: pourcentage de mortalité du sapin (*Abies balsamea* [L.] Mill.), volume mort total par essence hôte, surface terrière morte d'essences hôtes et surface terrière vivante d'essences hôtes. En pourcentage, la mortalité du sapin baumier a été environ deux fois plus importante que celle de l'épinette blanche (*Picea glauca* [Moench] Voss) ou de l'épinette noire (*Picea mariana* [Mill.] B.S.P.) dans les deux forêts nationales. La mortalité du sapin baumier en pourcentage a été extrêmement variable dans la forêt nationale d'Hiawatha. La mortalité du sapin baumier dans les peuplements à maturité est très élevée dans les districts de l'Est (74 à 90 %), tandis qu'elle est toujours inférieure à 25 % dans chacun des trois districts de l'Ouest. Ces différences très marquées dans la mortalité en pourcentage sont dues principalement à la présence d'excellents marchés pour la pâte du bois d'épinette et de sapin dans les districts de l'Ouest. Dans les districts de l'Est, l'absence de marché se traduit par une faible récolte du sapin. Dans la forêt nationale d'Ottawa, la mortalité en pourcentage du sapin, selon le district, a varié de 19 à 54 % jusqu'en 1983. En 1983, le volume mort total estimé de sapin baumier a atteint plus de 486 000 et 583 000 m^3 (17 et 20 millions de pieds cubes) dans les forêts nationales d'Hiawatha et d'Ottawa. Environ 90 et 84 % du volume mort total sont constitués de sapin. Au cours des cinq dernières années, une réduction de 36 et 30 % de la surface terrière vivante de sapin baumier a été constatée dans les forêts nationales d'Hiawatha et d'Ottawa respectivement.

Relationships Between Spruce Budworm and Spruce Coneworm

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The spruce coneworm (*Dioryctria reniculleloides* Mut. & Mun.), in association with the spruce budworm (*Choristoneura fumiferana* (Clem.)), appears to be an economically important pest of spruce in Maine. In

La pyrale des cônes de l'épinette (*Dioryctria renicullelloides* Mut. & Mun.), de concert avec la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]), semble un ravageur important du point de vue samples of overwintering larvae, distribution of both insects within tree crowns was similar, and midcrown branch samples are representative for both.

In a statewide survey of red spruce (*Picea rubens* Sarg.), coneworm comprised 16 to 30 percent of the coneworm-budworm complex in areas of both budworm outbreak and rareness. Correlation between numbers of the two species was $r = 0.87$. In stands of mixed spruce species, both insects were equally abundant on white spruce (*Picea glauca* (Moench) Voss) and red spruce; both insects were significantly less abundant on black spruce (*Picea mariana* (Mill.) B.S.P.).

Insect survey data from the Maine Forest Service showed that population oscillations of both insects have been parallel since 1949. Population numbers of both species are related spatially and temporally.

In forest sprayed with carbaryl, spruce budworm numbers on spruce were frequently reduced, but coneworm numbers were not. Coneworms increased by spraying and sometimes they were a majority of the surviving insects. Part of the difficulty in protecting red spruce with sprays is the failure to reduce spruce coneworm numbers.

économique de l'épinette dans le Maine. Dans des échantillons de larves hivernantes, la répartition des deux insectes dans les cimes d'arbres était semblable et les échantillons des branches situées au milieu de la cime sont représentatives des deux.

Dans une étude réalisée sur tout le territoire du Maine et portant sur l'épinette rouge (*Picea rubens* Sarg.), la pyrale des cônes de l'épinette constituait entre 16 et 30 % de l'ensemble pyrale-tordeuse, aussi bien dans les régions infestées par la tordeuse que dans les régions où la tordeuse était rare. La corrélation entre les nombres des deux espèces était $r = 0{,}87$. Dans les peuplements constitués d'essences d'épinettes mixtes, les deux insectes étaient aussi abondants dans l'épinette blanche (*Picea glauca* [Moench] Voss) que dans l'épinette rouge; les deux insectes étaient significativement moins abondants dans l'épinette noire (*Picea mariana* [Mill.] B.S.P.).

Des données de surveillance des insectes provenant du Service des forêts du Maine démontrent que les fluctuations de population des deux insectes suivent une courbe parallèle depuis 1949. L'importance des populations des deux espèces est reliée dans le temps et dans l'espace.

Dans les forêts où l'on a pulvérisé du carbaryl, on constate fréquemment une réduction du nombre de tordeuses dans les épinettes, mais non du nombre de pyrales. La proportion de pyrales augmentait après la pulvérisation, et parfois cette dernière constituait la majorité des insectes survivants. La difficulté qu'on éprouve pour protéger l'épinette rouge avec des pulvérisations d'insecticide est due au moins en partie à l'incapacité de réduire le nombre de pyrales des cônes de l'épinette.

Lepidoptera Associated with Western Spruce Budworm

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Populations of other lepidopterous species are oftern found along with those of western spruce budworm (*Choristoneura occidentalis* Freeman). Sometimes these "associates" are as numerous as budworms and have similar habits.

Field and laboratory workers need to be able to identify these associates, usually as larvae, sometimes as

D'autres lépidoptères sont souvent associés à la tordeuse occidentale de l'épinette. (*Choristoneura occidentalis* Freeman). Parfois, ils sont aussi nombreux que la tordeuse et possèdent des habitudes similaires.

Ceux qui travaillent sur le terrain et en laboratoire ont besoin de pouvoir les identifier, habituellement au stade larvaire, parfois adulte. La plupart des larves

adults. Most larvae can be differentiated from budworms with only a hand lens, or — if the larvae are large enough — with the naked eye. Adults are easier to identify.

Most common associates belong to the families Gelechiidae, Geometridae, Noctuidae, Plutellidae, Pyralidae, and Tortricidae. Some 30 species or species groups are represented in the cast of well-known associates.

Like budworms, these associates have dynamic populations. Species found in abundance one year can be rare the next, or numbers of a relatively unknown species can increase dramatically and qualify it as an associate.

peuvent être distinguées de celles des tordeuses, à la loupe seulement ou, si les larves sont assez grosses, à l'oeil nu. Les adultes sont plus faciles à identifier.

La plupart de ces lépidoptères appartiennent aux familles des Géléchiidés, des Géométridés, des Noctuidés, des Plutellidés, des Pyralidés et des Tortricidés. Quelque 30 espèces ou groupes d'espèces sont représentés dans le cortège des associés bien connus.

À l'instar de la tordeuse, les populations de ces insectes sont dynamiques. Les espèces abondantes une année peuvent être rares à la suivante, ou la population d'une espèce obscure peut s'accroître d'un coup et en faire une "associée" de la tordeuse.

Adaptation of Wax Moth Baculovirus to the Western Spruce Budworm

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An isolate of baculovirus (GmMNPV) from the greater wax moth (*Galleria mellonella*) was fed to neonate larvae of the western spruce budworm (*Choristoneura occidentalis* Freeman). Polyhedron development occurred only in the epithelial cells of the foregut and hindgut and the diseased larvae did not "wilt." The virus was extracted from these cells and fed to another group of neonate larvae. In these larvae, disease and polyhedra developed in many tissues and the larvae "wilted" upon death. Virus extracted from this group of larvae was found to be highly infectious for second and third instar western spruce budworm larvae. Furthermore, there was copious polyhedron development and the yield per diseased larva was very high. This "adapted" virus may prove to be more effective in suppressing budworm populations than any of the viruses isolated to date.

On a alimenté des larves néonates de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) avec un isolat de baculovirus (GmMNPV) provenant de la fausse-teigne de la cire (*Galleria mellonella*). La formation de polyèdres s'est produite seulement dans les cellules épithéliales de l'intestin antérieur et de l'intestin postérieur et les larves malades ne sont pas devenues flasques. Après avoir extrait le virus de ces cellules, on s'en est servi pour alimenter un autre groupe de larves néonates. Chez ces larves, la maladie et les polyèdres se sont manifestés dans de nombreux tissus; les larves sont devenues flasques au moment de la mort. Le virus extrait de ce groupe de larves s'est révélé très infectieux pour les deuxième et troisième stades larvaires de la tordeuse occidentale de l'épinette. De plus, il y avait une formation abondante de polyèdres et le rendement par larve malade était très élevé. Ce virus "adapté" pourrait se révéler le plus efficace des nombreux virus isolés jusqu'à présent pour lutter contre les populations de tordeuse.

Population Quality and the Biology of Two Western Budworms in Southern Oregon and Northern California

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Host specificity of sparse populations of western spruce budworm (*Choristoneura occidentalis* Freeman) and the Modoc budworm (*C. retiniana* Walsingham) in the Siskiyou Mountains, southern Cascade Range, and Gearhart Mountains was not strict. Western spruce budworm was previously thought to feed on both Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and true firs (*Abies* spp.) whereas Modoc budworm was thought to feed only on true firs. Population composition varied predictably with changes in forest composition. The coloration of these insects was significantly influenced by temperature. The degree that coloration is changeable depends on the sex and genetic background of the individual.

Temperature requirements for spring emergence, which synchronizes budworm feeding with host development, varied considerably among populations. In a mixed population of the two species, no clear association appeared between larval coloration and the pattern of spring emergence. Consequently, both Douglas-fir and true fir can be colonized by either species, even though host budflush may occur at different times.

Diel calling periodicities by females of the two species overlapped considerably. Furthermore, the courtship behavior of the species was indistinguishable. Apparently, the flight of males to female-produced pheromones is the primary mechanism causing reproductive isolation between these species. The degree of pheromone specificity is a function of release rate. Attractant specificities of known hybrids were similar to those of field-collected intermediate phenotypes. Post-mating reproductive barriers are not effective. The production of viable eggs from interspecific matings and the survival of progeny from these matings did not differ from those of conspecific matings. Evidently, reproductive barriers between these two species are not sufficient to completely isolate them when they occur together in mixed stands, but serve to structure populations in an unknown fashion.

This information will be useful in the development of more species-specific pest-management procedures for survey and control of these western budworms.

Les populations clairsemées de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) et de la tordeuse Modoc (*C. retiniana* Walsingham) des monts Siskiyou, des monts du sud des Cascades et des monts Gearhart n'avaient pas de strictes préférences d'hôtes. On croyait que la tordeuse occidentale de l'épinette s'alimentait du douglas taxifolié (*Pseudotsuga menziesii* [Mirb.] Franco) et du sapin (*Abies* spp.) et que la tordeuse Modoc ne s'alimentait que de sapin. La composition de leurs populations variait de façon prévisible selon celle des forêts. La couleur de ces insectes subit l'influence notable de la température, et son degré de modification dépend du sexe et du bagage génétique de chaque insecte.

Les températures nécessaires à l'émergence printanière, lesquelles synchronisent l'alimentation de la larve et le développement de l'hôte, variaient considérablement parmi les populations. Dans une population mixte des deux espèces, aucune association n'était évidente entre la coloration des larves et l'étalement des émergences. Le douglas et le sapin pouvaient donc être colonisés par les deux espèces, même si le débourrement pouvait survenir à des dates différentes.

La périodicité journalière de l'appel, chez les femelles des deux espèces, se recouvrait considérablement. De plus, il n'y avait aucun moyen de distinguer entre le comportement des deux espèces à la pariade. Apparemment, l'envol des mâles déclenché par les phéromones libérées par les femelles est le premier mécanisme d'isolement des deux espèces pour la reproduction. La spécificité des phéromones varie selon le taux de libération. La spécificité des attractifs d'hybrides connus était semblable à celle de phénotypes intermédiaires capturés sur le terrain. Les obstacles à la reproduction ne sont pas efficaces après l'accouplement. La production d'oeufs viables qui résultait d'accouplements interspécifiques et la survie de la progéniture qui en sortait n'ont pas différé de celles des accouplements intraspécifiques. Il est donc évident que les obstacles à la reproduction entre ces deux espèces ne suffisent pas à les isoler complètement lorsqu'elles habitent les mêmes peuplements mélangés, mais ils servent à structurer les populations d'une façon inconnue. Ces renseignements aideront à l'élaboration de méthodes de relevé et de contrôle spécifiques à ces tordeuses.

Comparative Dynamics of Sparse and Dense Western Budworm Populations

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Detailed studies of changes in density in successive stages of the western spruce budworm (*Choristoneura occidentalis* Freeman) were carried out in three populations in southern Oregon in 1978-80 and three populations in northern New Mexico in 1980-82. The Oregon populations were historically sparse; the populations in New Mexico encompassed a range of high densities in an area of general outbreak. Differences were shown in the patterns of survivorship within and between the stands in the respective areas. Survival rates in the larval and pupal periods differed significantly between the Oregon and New Mexico populations, with different parasitoid taxa assuming importance in each area. More detailed study of pupal mortality in two of the New Mexico study sites showed survival in this period can vary with tree crown level and within-site-characteristics. Variations in other quantitative population characteristics affecting the dynamics of this insect were also shown. Some implications to modeling and prediction of population change over space and time are discussed.

On a étudié en détail les variations successives de la densité de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) chez trois populations du sud de l'Oregon, de 1978 à 1080, et chez trois populations du nord du Nouveau-Mexique, de 1980 à 1982. En Oregon, les populations observées ont toujours été clairsemées; celles du Nouveau-Mexique passaient par toutes les gammes des densités élevées, dans une région d'infestation générale. On a observé des différences du taux de survie, dans les peuplements et entre les peuplements des régions respectives. La survie des larves et des chrysalides différait grandement entre les populations de l'Oregon et du Nouveau-Mexique, différents parasitoïdes jouant un rôle de premier plan dans chaque région. En raffinant l'étude de la mortalité des chrysalides dans deux des localités du Nouveau-Mexique, on a montré que la survie, au cours de ce stade, pouvait varier selon la hauteur dans le houppier et les caractéristiques locales. Les variations des autres caractéristiques mesurables des populations qui influent sur la dynamique de l'insecte sont aussi montrées. On discute de certaines de leurs répercussions sur la modélisation et la prédiction des variations spatio-temporelles des populations.

Radial Growth of Douglas-Fir Trees Defoliated by Western Spruce Budworm in Northern New Mexico

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Radial growth of trees infested with western spruce budworm (*Choristoneura occidentalis* Freeman) in the Carson National Forest, New Mexico, was assessed by dendrochronological analysis of increment cores extracted at breast height. Standardized and filtered Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)

On a déterminé la croissance en diamètre d'arbres infestés par la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman), dans la forêt nationale Carson, au Nouveau-Mexique, par analyse dendrochronologique de carottes prélevées à hauteur de poitrine. On a comparé les chronologies nor-

(host) and ponderosa pine (*Pinus ponderosa* Laws.) (non-host) tree-ring chronologies were compared. Douglas-fir growth was reduced during past and current budworm outbreaks. The non-host tree-ring chronologies were used to remove non-budworm effects such as climate from the host tree-ring chronologies. The corrected chronologies where then used to assess growth losses during known budworm outbreaks. The maximum growth-loss during 1 year was generally greater than 50 percent of expected growth. The average growth loss for 5-year periods during outbreaks was about 30 to 40 percent of expected growth, and the maximum growth loss between 2 years of an outbreak was usually more than 50 percent of expected growth.

The dendrochronological techniques of crossdating, standardization, filtering, and correction for non-budworm effects provide a high degree of reliability and precision to budworm-induced growth-loss estimates. Most of these procedures and techniques have been used for many years in dendroclimatic and dendroecologic studies; however, this study marks the first time they have been applied, in combination, to an insect-defoliation study. In addition to impact study on budworm and other insects, these techniques have potential application in assessing effects on tree growth of pollution and other environmental factors.

malisées et filtrées des cernes de douglas taxifoliés (*Pseudotsuga menziesii* [Mirb.] Franco) (essence hôte) et de pins ponderosa (*Pinus ponderosa* Laws.) (essence non hôte). Durant les infestations actuelles et antérieures de la tordeuse, la croissance du douglas a été ralentie. L'étude dendrochronologique des arbres non hôtes a permis d'éliminer les effets non attribuables à la tordeuse, tels que ceux du climat, exercés sur les hôtes, puis les chronologies corrigées ont servi à évaluer les pertes de croissance au cours d'infestations connues. La perte maximale de croissance en une année était généralement supérieure à 50 % de la croissance prévue. La perte moyenne de croissance au bout de 5 ans, au cours d'infestations, était environ de 30 à 40 % de la croissance prévue, et la perte maximale de croissance entre deux années d'une infestation était habituellement supérieure à 50 % de la croissance prévue.

Les techniques dendrochronologiques d'appariement des dates, de normalisation, de filtrage et de correction des effets non attribuables à la tordeuse procurent un haut degré de fiabilité et de précision aux estimations des pertes de croissance causées par la tordeuse. La plupart de ces méthodes et techniques ont servi pendant de nombreuses années aux études dendroclimatiques et dendro-écologiques; toutefois, la présente étude est la première où elles servent toutes les deux à l'étude de la défoliation par un insecte. Ces techniques ne permettent pas seulement d'étudier les répercussions des tordeuses et d'autres insectes, mais elles peuvent aussi servir à évaluer les effets sur la croissance des arbres de la pollution et d'autres facteurs naturels.

How to Distinguish Between Old and New Egg Masses of the Western Spruce Budworm

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Sampling egg masses of western spruce budworm (*Choristoneura occidentalis* Freeman) is an accepted method of estimating population density. A critical aspect of the sampling procedure is the ability to distinguish the current year's egg-mass population from that deposited in a previous year. Distinguishing new from old egg masses requires proper branch handling and attention to several characteristics, including shape, color, and location of the egg mass.

L'échantillonnage des masses d'oeufs de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) est une méthode acceptée d'estimation de la densité de ses populations. Un aspect critique en est la possibilité de distinguer celles de l'année de celles d'une année antérieure. À cette fin, la manutention convenable des branches et l'observation soigneuse de plusieurs caractéristiques, y compris la forme, la couleur et l'emplacement des masses, sont essentielles.

The Shelterwood Simulator

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The Shelterwood Simulator is a mechanical poster display that requires active viewer participation. Flip panels, photographs, a chart, and the four three-dimensional forest models in the carousel are color-keyed to each other. The message emerges as the viewer flips the panels and rotates the carousel.

Viewers learn that the shelterwood system of silviculture is perhaps the best and least risky way to regenerate a spruce-fir stand. By employing shelterwood principles, followed by early timber-stand-improvement work, managers can ensure that new stands containing a larger component of the less vulnerable and more valuable spruce can be attained in 10 to 20 years. The three-stage method requiring the preparatory, seed, and removal stages is presented in the Simulator. The information is from long-term research results at the Penobscot Experimental Forest near Bangor, Maine.

The Simulator is a product of a technology transfer project sponsored by CANUSA and coordinated by the College of Forest Resources, University of Maine, and the USDA Forest Service, both in Orono, Maine.

Le simulateur du mode de régénération par coupes progressives constitue un ensemble d'affiches mécaniques qui nécessite une participation active des spectateurs. Des panneaux basculants, des photographies, un graphique et quatre modèles forestiers tridimensionnels dans un caroussel sont reliés entre eux par un code couleur. Le message apparaît lorsque le spectateur bascule les panneaux et fait tourner le caroussel.

Le spectateur apprend que le mode de régénération par coupes progressives est peut-être le meilleur système sinon le plus sûr pour régénérer un peuplement d'épinette et de sapin. En appliquant les principes inhérents à ce système de régénération, et en pratiquant rapidement des travaux d'amélioration des peuplements de bois, les gestionnaires peuvent s'assurer que les nouveaux peuplements contiendront une plus grande proportion d'épinettes moins vulnérables et de plus grande valeur dans dix à vingt ans. La méthode en trois étapes comprenant la coupe préparatoire, la coupe d'ensemencement et la coupe secondaire est présentée à l'aide du simulateur. L'information véhiculée provient des résultats de recherches à long terme réalisées dans la forêt expérimentale de Penobscot près de Bangor, dans le Maine.

Le simulateur est un produit résultant du projet de transfert de technologie parrainé par le programme CANUSA et coordonné par le *College of Forest Resources*, Université du Maine, et le *USDA Forest Service*, tous deux d'Orono, dans le Maine.

Black Spruce Mortality and Survival Following Spruce Budworm Defoliation and Attack by Secondary Pests in Newfoundland

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Generally black spruce (*Picea mariana* (Mill.) B.S.P.) has been considered as one of the least vulnerable host species to spruce budworm (*Choristoneura fumiferana* (Clem.)) defoliation because it has usually survived previous outbreaks of this pest. The recent

On a longtemps considéré l'épinette noire (*Picea mariana* [Mill.] B.S.P.) comme l'hôte le moins vulnérable à la défoliation par la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]); dans le passé, elle avait survécu à plusieurs attaques. Or, la

outbreak in Newfoundland was unprecedented in size and severity and almost all black spruce stands were severely defoliated for 3 to 5 years resulting in widespread branch tip mortality, top kill, and some tree mortality. Most of these stands showed good recovery for 2 to 3 years following the collapse of budworm populations. However, in 1982 a general deterioration of trees and increased mortality occurred in many black spruce stands. This trend expanded and increased in intensity in 1983. The four-eyed spruce bark beetle (*Polygraphus rufipennis* Kby.) and Armillaria root rot by *Armillaria mellea* (Vahl ex Fr.) Kummer, hastened tree mortality in these stands. Black spruce mortality in relation to age and site characteristics, severity of budworm damage, and intensity of attack by bark beetles and root rot are analyzed and discussed.

récente épidémie survenue à Terre-Neuve était jusqu'à présent, de par sa taille et sa gravité, sans précédent. En effet, presque tous les peuplements d'épinette noire ont subi une défoliation avancée durant trois à quatre ans, entraînant une mortalité répandue des bouts de branches, un dépérissement de la cime voire même la mort de certains arbres. Mais, la plupart de ces peuplements se sont rétablis au cours des deux ou trois années suivant l'effondrement des populations de tordeuses. Toutefois, en 1982, on a noté une détérioration générale des arbres et une mortalité fortement accrue dans de nombreux peuplements d'épinette noire, et ce phénomène a pris de l'ampleur en 1983. On a constaté que le polygraphe de l'épinette (*Polygraphus rufipennis* [Kby.]), et le pourridié-agaric (*Armillaria mellea* [Vahl ex Fr.] Kummer) hâtaient la mort des arbres dans ces peuplements. Dans la présente communication, on traitera de la mortalité de l'épinette noire en fonction de l'âge et des caractéristiques du site, de la gravité des ravages causés par la tordeuse, et de l'intensité de l'attaque par les polygraphes et le pourridié.

Biological Mortality Factors of the Spruce Budworm in Newfoundland

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The recent outbreak of the spruce budworm (*Choristoneura fumiferana* (Clem.)) in Newfoundland commenced in 1972 and had collapsed in most regions by 1984. Budworm population levels and the extent and severity of defoliation peaked in 1976 and 1977. The outbreak began to collapse in 1981 and continued to decline to 1984. Population levels of the spruce budworm and several biological mortality factors were sampled throughout the outbreak. Thirteen bird species fed on spruce budworm larvae and pupae but they had little control value during the outbreak. Only eight insect parasite species of the budworm are common in Newfoundland. Parasitism by these species increased gradually from the beginning of the outbreak, but they failed to control the increasing budworm populations. Five species of pathogens were infecting budworm larvae and pupae. These were four fungi: *Entomophthora egressa* MacLeod and Tyrrell, *Erynia radicans*

La dernière infestation de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) à Terre-Neuve, qui a débuté en 1972, a pris fin dans la plupart des régions avant 1984. Les effectifs de la tordeuse et la défoliation ont culminé en 1976 et 1977. Le déclin a commencé en 1981 et s'est poursuivi jusqu'en 1984. Durant l'infestation, on a mesuré, par échantillonnages, les effectifs et plusieurs facteurs naturels de mortalité. Treize espèces d'oiseaux se nourrissent des larves et des chrysalides de la tordeuse, mais leur influence a été très modeste. À Terre-Neuve, on ne trouve que huit insectes parasites communs de la tordeuse. Depuis le début de l'infestation, leur rôle a graduellement pris de l'importance, sans toutefois être efficace. Cinq pathogènes infectent les larves et les chrysalides: quatre champignons microscopiques, *Entomophthora egressa* MacLeod et Tyrrell, *Erynia radicans* (Brefeld) Humber,

(Brefeld) Humber, Ben-Zéev and Kenneth, *Hirsutella gigantea* Petch and *Paecilomyces farinosus* (Holm ex S.f. Gray) Brown and Smith, and a microsporidian, *Nosema fumiferanae* (Thomson). Infection by those organisms increased during the outbreak and reached over 50 percent in localized areas, but their overall control of the outbreak was not significant. In 1981 during the collapse of the spruce budworm populations, a high proportion of fourth and fifth instar larvae died of unknown causes. Competition or lack of food were not considered as the cause of this mortality and viruses have not been recorded in the spruce budworm in Newfoundland.

Laboratory research and small scale field tests indicated that artificial mass production and application of insect pathogenic fungal spores has good potential to control budworm populations. In laboratory experiments the nematode, *Heterorhabditis heliothidis* (Khan, Brooks and Hirschmann) caused high level of mortality in spruce budworm larvae and pupae. A cold tolerant strain of the nematode, *Neoaplectana bibionis* Bovien, was pathogenic at 8°C. The potential use of these nematodes to control spruce budworm populations is being investigated.

Ben-Zéev et Kenneth, *Hirsutella gigantea* Petch et *Paecilomyces farinosus* (Holm ex S.f. Gray) Brown et Smith; une microsporidie, *Nosema fumiferanae* (Thomson). L'incidence de l'infection par ces pathogènes a augmenté durant l'infestation, pour atteindre 50 % dans certaines localités, mais, dans l'ensemble, l'infestation n'a pas été notablement réprimée. En 1981, alors que l'infestation diminuait, une forte proportion des larves du 4^e et du 5^e stade sont mortes de causes inconnues. La concurrence ou le manque de nourriture ont été écartées comme causes, tandis qu'on n'a pas observé de virus de la tordeuse à Terre-Neuve.

La recherche en laboratoire et des essais sur le terrain, à petite échelle ont montré que la fabrication artificielle et l'application en masse de spores de champignons pathogènes étaient prometteuses contre la tordeuse. Au laboratoire, le nématode *Heterorhabditis heliothidis* (Khan, Brooks et Hirschmann) a tué une forte proportion de larves et de chrysalides de la tordeuse. Une souche du nématode *Neoaplectana bibionis* Bovien, tolérant le froid, a agi à 8 °C. On examine la possibilité d'utiliser ces nématodes contre la tordeuse.

Economic Impact of the Spruce Budworm in the Lake States

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Economic effects of spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks in the Lake States have not been well understood, although the physical impact has been estimated. Long and short run responses of spruce-fir supply and demand to spruce budworm outbreaks were examined. Estimates of the value of spruce-fir losses on the National Forests in Michigan's Upper Peninsula were calculated by district. Economic impact of spruce budworm outbreaks and market conditions were found to be directly related.

Bien qu'on ait évalué les conséquences physiques de la pullulation de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]), dans les États des Grands lacs, on connaît encore mal les conséquences économiques qu'elle entraîne. On a examiné les réactions à court et à long termes de l'offre et de la demande ayant trait à l'épinette et au sapin en rapport avec la pullulation de la tordeuse. On a estimé la valeur des pertes en épinettes et en sapins dans les forêts fédérales de la Haute péninsule du Michigan par district. Nous avons constaté que l'impact économique de la pullulation de la tordeuse et les conditions du marché étaient directement reliés.

Rating Spruce-Fir Stands in Michigan's Upper Peninsula for Hazard from the Spruce Budworm

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The estimated potential effect on balsam fir (*Abies balsamea* (L.) Mill.) basal area is presented for three geographic regions in Michigan's Upper Peninsula. Potential dead balsam fir basal area in the eastern Upper Peninsula is estimated as a function of preoutbreak balsam fir basal area and the percentage of aspen (*Populus* L. spp.) in the stand. Mean dead balsam fir basal area per hectare is used to estimate the potential impact in the central portion of the peninsula. Dead balsam fir basal area in stands in the western Upper Peninsula with at least 10 m^2 per hectare of balsam fir basal area is estimated as a function of preoutbreak fir and stand position on an east-west gradient (range). The mean dead balsam fir basal area per hectare is used to estimate potential impact in stands in the western Upper Peninsula with less than 10 m^2 per hectare of balsam fir basal area. Stands can be indexed or ranked according to the estimates of potential losses. The relative hazard rank can then be used to select stands for preventive silvicultural treatments, presalvage and salvage harvest operations, or for remedial treatments.

On présente l'impact potentiel estimé de la surface terrière d'un peuplement de sapin baumier (*Abies balsamea* [L.] Mill.) pour trois régions géographiques de la Haute péninsule du Michigan. La surface terrière potentielle des sapins baumiers morts dans la partie est de la Haute péninsule est évaluée en fonction de la surface terrière des sapins baumiers avant pullulation et du pourcentage de peupliers faux-trembles (*Populus* L. spp.) dans la composition du peuplement. La surface terrière moyenne des sapins baumiers morts par hectare est utilisée pour évaluer l'impact potentiel dans la partie centrale de la péninsule. La surface terrière des sapins baumiers morts dans les peuplements de la partie ouest de la Haute péninsule avec au moins 10 m^2/ha de surface terrière de sapin baumier est estimée en fonction de la position du sapin et du peuplement sur un gradient est-ouest (étendue) avant la pullulation. La surface terrière moyenne d'un peuplement de sapin baumier mort par hectare sert à estimer l'impact potentiel dans les peuplements de la partie ouest de la Haute péninsule ayant moins de 10 m^2/ha de surface terrière de sapin baumier. Les peuplements peuvent être classés ou cotés en fonction des estimations des pertes potentielles. Le classement relatif peut alors être utilisé pour établir des priorités quant aux traitements sylvicoles à caractère préventif, aux opérations de récupération et de prérécupération de même qu'aux traitements curatifs.

The Spruce Budworm Technology Transfer Program for the Lake States Region: The Project Methodology

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The Spruce Budworm Technology Transfer Program for the Lake States Region was a prototypical technology transfer project. The major methodology consisted of three phases: 1) the administration of two needs-assessment surveys of the project target audiences; 2) development and implementation of the spruce budworm information/educational packages and activities;

Le programme de transfert de technologie relatif à la tordeuse des bourgeons de l'épinette pour la région des États des Grands lacs était un projet pilote. La méthode principale comportait trois phases: (1) la réalisation de deux enquêtes pour évaluer les besoins des auditoires visés par le projet; (2) la mise au point et la mise en application d'activités et de programmes

and 3) formal and informal evaluation of these products and activities. The key to effective implementation of this methodology has been active target audience input into all three phases. This is the one component that has contributed the most to the success of the project.

d'information et d'éducation sur la tordeuse des bourgeons de l'épinette; et (3) l'évaluation formelle et informelle de ces produits et activités. La clé du succès pour la mise en application de cette méthode est la participation active des auditoires visés au cours des trois phases du projet. C'est l'élément qui a contribué le plus au succès du projet.

Pheromone Dispensers and Trap Designs for Monitoring Spruce Budworm Populations

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The potential of sex pheromone traps for monitoring spruce budworm (*Choristoneura fumiferana* (Clem.)) populations is well established. For results to be comparable the system must be standardized and unchanged from year to year. It is therefore important to ensure that the best available system is implemented from the start.

Various commercial lures are available, all are adequate and choice will depend upon cost and availability. Although sticky-coated traps (e.g., Pherocon 1C) are effective at low density populations, they quickly 'saturate' at higher densities. Attention has therefore switched to 'non-saturating' designs. 'Home-made' designs have proven effective, but a commercially available trap has merit for extensive use.

Commercial designs have been compared with 'home-made' traps in a laboratory wind-tunnel and in the field. Desirable attributes are adequate catch and low variation in catch among traps. On the assumption that variability will be lowest when moths enter the trap quickly and cannot easily escape, the best design is one in which the air flow through the trap produces a discrete pheromone plume, and which has a 'lobster pot' baffle to prevent moths escaping.

La valeur des pièges utilisant des phéromones sexuelles pour la surveillance des populations de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) est maintenant bien établie. Pour que les résultats soient comparables, le système doit être normalisé et doit demeurer le même d'une année à l'autre; par conséquent, il est important de s'assurer que le meilleur système disponible soit utilisé dès le début.

Il existe divers pièges commerciaux sur le marché; ils sont tous appropriés et le choix de l'un d'entre eux dépend du coût et de la disponibilité. Bien que les pièges englués (Pherocon IC) soient efficaces lorsque la densité de population est faible, ils deviennent vite "saturés" lorsque les densités sont élevées. Ainsi, l'attention s'est portée sur les systèmes qui ne risquent pas d'être saturés. Des systèmes de fabrication artisanale se sont révélés efficaces, mais il existe un piège disponible commercialement qui se prête bien à une utilisation intensive.

Les systèmes commerciaux ont été comparés aux pièges de fabrication artisanale en soufflerie et sur le terrain. Les caractéristiques recherchées sont une prise acceptable et une faible variation dans les prises d'un piège à l'autre. En supposant que la variabilité sera plus faible lorsque les insectes peuvent entrer rapidement dans les pièges et ne peuvent en sortir facilement, la meilleure conception est celle qui, sous l'effet de la circulation d'air dans le piége, produit des émanations délicates de phéromone et qui est munie d'une chicane comme celle que l'on retrouve dans les casiers à homards, pour empêcher les insectes de s'échapper.

The Relation of Climate to Frequency of Western Spruce Budworm Outbreaks

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Selected climatic variables and regional western spruce budworm were studied to determine if they were related to outbreak frequency of *Choristoneura occidentalis* Freeman in Idaho, Montana, Oregon, and Washington. Defoliation histories from 43 points throughout the four States were used to identify three broad regional compartments of differing outbreak frequencies. Mean maximum and minimum temperatures for January and July, as well as mean annual precipitation data, were collected from a four-State stratified sample of 169 points where susceptible forest type occurred. Significant differences were found in climate between the three classes of outbreak frequencies identified. A discriminant analysis was developed to predict the outbreak frequency of any point in the four-State area as a function of the climatic characteristics of each point. These findings should be useful to forest managers and researchers interested in the regional characteristics of budworm outbreak-frequency.

On a étudié, à l'échelle régionale, certaines variables climatiques pour déterminer si on pouvait les corréler à la fréquence des infestations de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) dans l'Idaho, le Montana, l'Oregon et le Washington. Les antécédents de la défoliation en 43 localités de ces États ont permis de délimiter trois grandes régions où la fréquence des infestations différait. Dans un échantillonnage stratifié de 169 stations en forêts vulnérables dans ces États, on a recueilli des renseignements sur les températures moyennes maximales et minimales en janvier et juillet ainsi que sur la pluviosité annuelle moyenne. Des différences climatiques notables ont été observées entre les trois classes de fréquence de pullulation. Une méthode d'analyse discriminante a été mis au point pour prédire la fréquence des pullulations dans tous les points des quatre États, en fonction de ces caractéristiques climatiques. Ces résultats pourraient servir aux aménagistes et aux chercheurs forestiers qui s'intéressent aux caractéristiques régionales de la fréquence des pullulations de la tordeuse.

Coniferous Forest Succession in Newfoundland following Severe Defoliation by the Spruce Budworm

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Forest succession in Newfoundland after severe spruce budworm (*Choristoneura fumiferana* (Clem.)) infestation was monitored using a combination of rapid survey technique (point-centered quarter) and remeasurement of permanent sample plots. The rapid survey technique can be used to document damage in all vegetation strata of the forest and predict future stand composition on the basis of residual tree populations. Permanent sample plots provide a means of monitoring long-term changes in stand composition due to budworm infestation as well as other natural causes.

Even where tree mortality approaches 100 percent, budworm damage rarely penetrates the lower tree

La succession des forêts à Terre-Neuve après une infestation importante par la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) a été étudiée en combinant une technique de sondage rapide (quartier centré sur un point) et le remesurage de parcelles d'échantillonnage permanentes. La technique de sondage rapide peut être utilisée pour vérifier les dégâts dans toutes les strates de végétation d'une forêt et prévoir l'éventuelle composition d'un peuplement à partir des populations d'arbres qui restent. Les parcelles d'échantillonnage permanentes fournissent un moyen de suivre les changements à long terme dans la composition d'un peuplement à la suite d'une strata (less than 3 m). In most balsam fir (*Abies balsamea* (L.) Mill.) stands advance coniferous regeneration is in excess of 30,000 stems per hectare. However, on high capability sites fir advance growth can be overtopped by up to 18,000 stems per hectare of white birch (*Betula papyrifera* Marsh.) saplings. Such changes in future stand composition can have a dramatic negative effect on the merchantability of these forests for pulpwood.

In pure black spruce (*Picea mariana* (Mill.) B.S.P.) forests of fire origin with severe infestation, merchantable tree mortality in 1983 ranged from 30 to 50 percent and nonomerchantable mortality varied from 10 to 30 percent. These forests do not have sufficient advance growth or seed crop to ensure adequate regeneration. Succession to ericaceous dwarf heath may occur if remedial silvicultural treatments are not undertaken in the near future.

infestation par la tordeuse ou d'autres phénomènes naturels.

Même lorsque la mortalité des arbres atteint presque 100 %, les dommages causés par la tordeuse ne se manifestent que rarement dans la strate inférieure des arbres (moins de 3 m). Dans la plupart des peuplements de sapin baumier (*Abies balsamea* [L.] Mill.), la régénération préexistante de conifères dépasse 30 000 tiges par hectare. Toutefois, dans des sites ayant une capacité élevée, la régénération préexistante de sapin peut être dépassé par 18 000 tiges par hectare de pousses de bouleau à papier (*Betula papyrifera* Marsh.). De tels changements dans la composition future du peuplement peuvent encourir des conséquences néfastes sur la valeur marchande de ces forêts, en égard à la production des bois de pâte.

Dans un peuplement pur d'épinette noire (*Picea mariana* [Mill.] B.S.P.), régénéré après un incendie et ayant subi une grave infestation, la mortalité des arbres ayant une valeur marchande a varié, en 1983, de 30 à 50 %, et celle des arbres dépourvus de valeur marchande, de 10 à 30 %. Ces forêts n'ont pas de régénération préexistante ou d'ensemencement suffisants pour assurer une régénération appropriée. Par conséquent, si des mesures sylvicoles appropriées ne sont pas prises dans un avenir rapproché, il pourrait en résulter une succession d'éricacées.

Western Spruce Budworm Population Dynamics Model

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A model has been developed that stimulates the population dynamics of the western spruce budworm (*Choristoneura occidentalis* Freeman). The modeling approach was chosen to integrate the various studies supported by CANUSA-West and provide a coherent means for using results. The western spruce budworm

Un modèle de la dynamique des populations de la tordeuse occidentale de l'épinette (*Choristoneura occidentalis* Freeman) a été mis au point pour intégrer les résultats des diverses études financées en vertu du programme CANUSA-Ouest et les utiliser de façon cohérente. Le modèle Tordeuse occidentale (Budworm

population dynamics model (Budworm Model) has two major components. The submodel BWMOD simulates population dynamics from egg hatch to adult emergence. The submodel BWFLY simulates moth dispersal and oviposition. When linked to the Prognosis Model, the Budworm Model may be used to predict budworm-caused damage under various stand conditions. The Budworm Model may also be used to evaluate probable effects of various treatments (silvicultural manipulation or insecticide application) on subsequent damage. The aggregation of individual simulations can provide forest managers and planners with information necessary for the development of comprehensive resource plans for large geographic areas, such as National Forests. The Budworm Model may also be used by research scientists to define future research priorities and improve our understanding of the complex environment in which the western spruce budworm resides.

model) possède deux éléments principaux: l'élément BWMOD simule la dynamique des populations, de l'éclosion des oeufs à l'émergence des adultes; l'élément BWFLY simule la dispersion des papillons et la ponte. Accouplé au modèle Prognosis, le modèle peut servir à prévoir les dommages causés par la tordeuse dans diverses conditions de peuplements, ainsi que les répercussions de divers traitements (sylvicoles ou insecticides) sur les dommages ultérieurs. Par une série de simulations, les aménagistes et les planificateurs peuvent tirer les renseignements nécessaires à la planification détaillée de la mise en valeur des ressources de vastes régions géographiques telles que les forêts nationales. Le modèle peut aussi servir aux chercheurs pour déterminer les priorités à venir de la recherche et améliorer notre compréhension de l'habitat complexe de la tordeuse.

Biodeterioration in Balsam Fir Killed by Spruce Budworm in Newfoundland

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Hirschioporus abietinus (Dicks. ex Fr.) Donk and *Amylostereum chailletii* (Pers. ex Fr.) Boid are two major fungi causing defects in balsam fir (*Abies balsamea* (L.) Mill.) damaged by spruce budworm (*Choristoneura fumiferana* (Clem.)) in Newfoundland. The most significant defect is an advanced, white sap rot caused by *H. abietinus* whereas *A. chailletii* is responsible for a red-brown stain and incipient decay. Secondary insects apparently are the major contributing factors to the establishment of both of these fungi. The balsam fir bark beetle (*Pityokteines sparsus* (LeC.)) is a factor in the early establishment of *H. abietinus* in the outer sapwood region of killed trees resulting in advanced decay as early as 2 years. *A. chailletii* is innoculated into the dying trees during oviposition by siricid woodwasps. This fungus becomes rapidly established within the sapwood region and *H. abietinus* establishment in these trees may be delayed as long as 3-4 years. Rates of deterioration of dead balsam fir may vary between western and central Newfoundland due to the differences in secondary insect activity. In

Hirschioporus abietinus (Dicks. ex Fr.) Donk et *Amylostereum chailletii* (Pers. ex Fr.) Boid. sont deux champignons importants entraînant des anomalies chez les sapins baumiers endommagés par la défoliation par la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* [Clem.]) à Terre-Neuve. L'effet le plus important est une carie blanche avancée causée par *H. abietinus*, tandis qu'*A. chailletii* provoque une tache rouge-brun et développe une carie de stade initial. Les insectes secondaires seraient apparemment les principaux facteurs contribuant à l'émergence de ces deux champignons. Le scolyte du sapin baumier (*Pityokteines sparsus* [LeC.]) joue un rôle dans le développement précoce de *H. abietinus* dans la région externe de l'aubier des arbres tués, ce qui entraîne une carie avancée en l'espace de deux ans seulement. *A. chailletii* est inoculé dans les arbres mourants durant l'oviposition par les sirex. Le champignon s'établit rapidement dans la région de l'aubier et l'installation de *H. abietinus* dans ces arbres peut être retardée de trois à quatre ans. Les taux de détérioration-

central Newfoundland higher bark beetle activity correlates with the early presence and significant advanced decay losses due to *H. abietinus* as compared to western Newfoundland with lower bark beetle and higher siricid woodwasp activity. In salvage using cut and skid operations, breakage of stems dead for up to 2 years were 21 and 51 percent in mature and overmature trees respectively as compared to 48 and 91 percent in stems dead for more than 2 years. The more frequent stem breakage increased the volume of logging residue from 5 percent of the stand volume in stands dead for up to 2 years to 20 percent or more in stands dead for more than 2 years.

tion des sapins baumiers morts peuvent varier entre la partie ouest et la partie centrale de Terre-Neuve à cause de la différence dans l'activité des insectes secondaires. Dans la partie centrale de Terre-Neuve, une activité plus grande des scolytes correspond à la présence précoce de *H. abietinus* et à des pertes importantes dues à la carie avancée, tandis que dans l'ouest de Terre-Neuve, l'activité des scolytes est plus faible et celle des sirex plus grande. Dans les opérations de récupération par coupe et débusquage, les bris de tiges mortes depuis moins de deux ans étaient respectivement de 21 et 51 % dans les arbres à maturité ou à surmaturité, comparativement à 48 et 91 % dans le cas des tiges mortes depuis plus de deux ans. La fréquence des bris de tiges augmente les résidus de coupe de 5 % du volume des peuplements, dans le cas des peuplements morts depuis moins de 2 ans, à 20 % ou plus, dans le cas des peuplements morts depuis plus de 2 ans.

Some Effects of Pesticide Formulations on the Phytobiota of Forest Ecosystems

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Atlox 3409F, Aerotex 3470, Nonylphenol, Cyclosol 66, Dowanal, and diesel oil 585 are added as inert solvents/detergents to pesticide formulations. The toxicity of these adjuvants on the phytobiota of forest ecosystems was tested. The parameters assessed included the growth and development of three nontarget tree seeds, jack pine (*Pinus banksiana* Lamb.), white birch (*Betula papyrifera* Marsh.), and yellow birch (*B. alleghaniensis* Britton), and flagellate alga *Chlamydomona reinhardtii* Dang.)

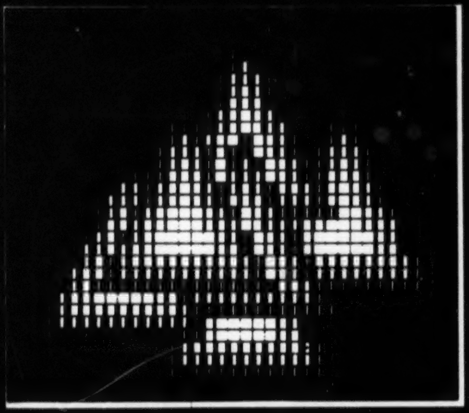
Generally, Dowanol >100 μg/mL, the pesticides, and 585 oil>40μg/mL were nontoxic. Aerotex, Nonylphenol, and Cyclosol 66 were highly toxic >0.75 μg/mL. Growth, development, and ultrastructure were negatively affected by these agents in the nontarget forest seeds and aquatic alga. The inert solvents/detergents in the formulations perturbed these organisms more than the active pesticides.

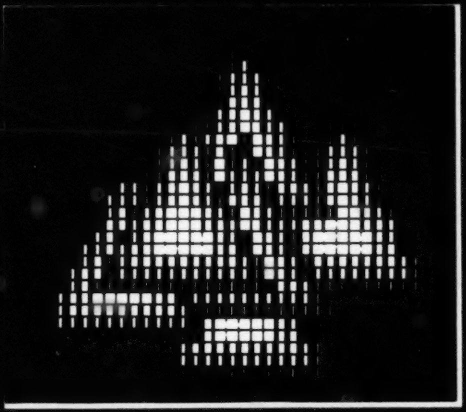
L'Atlox 3409F, l'Aerotex 3470, le Nonylphénol, le Cyclosol 66, le Dowanol et l'huile diesel 585 sont ajoutés comme solvants/détergents "inertes" dans les préparations de pesticides. La toxicité de ces adjuvants pour les écosytèmes forestiers a été testée. Parmi les paramètres examinés, on compte la croissance et le développement des graines de trois essences non cibles, le pin gris (*Pinus banksiana* Lamb.), le bouleau à papier (*Betula papyrifera* Marsh.), le bouleau jaune (*B. alleghaniensis* Britton) et l'algue flagellée ubiquiste (*Chlamydomona reinhardtii* Dang).

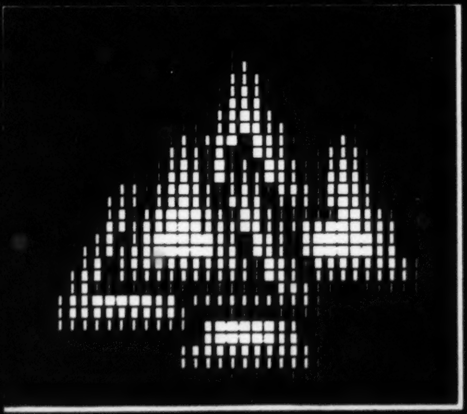
Généralement, le Dowanol à >100μg/mL, les pesticides et l'huile diesel 585 à >40μg/mL n'étaient pas toxiques. L'Aerotex, le Nonylphénol et le Cyclosol 66 étaient hautement toxiques à 0,75 μg/mL. La croissance, le développement et l'ultrastructure des graines d'essences non cibles et de l'algue aquatique ont subi des effets défavorables. Les ingrédients "inertes" ont perturbé davantage ces organismes que les ingrédients "actifs" des pesticides.

Part VII

Appendices







Program

Sunday, September 16

1500-2400 Arrival and Registration (Holiday Inn, Main Street)

1900-2100 Reception (Holiday Inn, Main Street)

Monday, September 17

0800-1700 Registration (Civic Center)

0830 Welcoming Remarks and Announcements: F.B. Knight, Associate Dean, College of Forest Resources, University of Maine at Orono, Orono, Maine

0845-0930 **CANUSA: beginning to end,** K.R. Shea, Associate Deputy Chief for Research, USDA Forest Service, Washington, D.C.; and C.H. Winget, Director General, Research and Technical Services, Canadian Forestry Service, Ottawa, Ontario

0930-1500 *Invitational Papers*

Theme: ***Spruce budworms — Biology, ecology, and population dynamics***

Moderator: W.L. Sippell (Retired), Canadian Forestry Service, Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario

1. ***Taxonomic status of Choristoneura spp.,*** G.T. Harvey, Canadian Forestry Service, Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario
2. ***The ecology of the eastern spruce budworm: a review and discussion,*** J.R. Blais (Retired), Canadian Forestry Service, Laurentian Forest Research Centre, Sainte-Foy, Quebec
3. ***The western spruce budworm: strategy for survival,*** R.F. Shepherd, Canadian Forestry Service, Pacific Forest Research Centre, Victoria, British Columbia
4. ***Commonalities and differences between eastern and western spruce budworms,*** W.J.A. Volney, Canadian Forestry Service, Winnipeg, Manitoba

1500-1830 **Workshop I—Population Dynamics. How close are we to predicting the occurrence, severity and duration of budworm outbreaks?**

Moderator: M.W. McFadden, International Forestry, USDA Forest Service, Washington, D.C.

(*The name following the subject area is that of the Discussion Leader.*)

A. ***What are the roles in regulating:***

Environmental factors, A.J. Thomson, Canadian Forestry Service, Victoria, British Columbia

Predators, R.W. Campbell, USDA Forest Service, Corvallis, Oregon

Parasites, M. Houseweart, University of Maine, Orono, Maine

Diseases, D. Perry, Canadian Forestry Service, Ste-Foy, Quebec

Budworm behavior, R.C. Beckwith, USDA Forest Service, La Grande, Oregon

Host-plant interactions, W.J. Mattson, USDA Forest Service, East Lansing, Michigan

B. ***What can we learn from historical records and what are the theoretical interpretations?*** C.J. Sanders, University of New Brunswick, Fredericton, New Brunswick

Tuesday, September 18

0830-1200 *Invitational Papers*

Theme: ***Economic and social impacts of spruce budworms in North American forests***

Moderator: R.H. Tremblay, Advisor to the Deputy Minister (Lands and Forests), Department of Energy and Resources, Quebec, Quebec

5. ***Impact of the spruce budworms on forest productivity,*** D.A MacLean, Canadian Forestry Service, Maritimes Forest Research Centre, Fredericton, New Brunswick
6. ***Economic consequences of budworm outbreaks,*** T.D. Bible, California State University, Los Angeles, California
7. ***Budworm damage and fire hazard,*** B.J. Stocks, Canadian Forestry Service, Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario
8. ***Forecasting growth and yield of budworm infested forests,*** N.L. Crookston, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, Idaho; and R.S. Seymour, College of Forest Resources, University of Maine, Orono, Maine

1300-1700 **Workshop II — Population and Impact Assessment**

Moderator: W.E. Waters, University of California, Berkeley, California

Theme: ***Are our current techniques adequate? What new or modified techniques are available for:***
A. ***Determining insect numbers,*** A.G. Raske, Canadian Forestry Service, St. John's Newfoundland
B. ***Quantifying impacts on forest growth and yield,*** D.S. Solomon, USDA Forest Service, Orono, Maine
C. ***Quantifying impacts on other forest resources (recreation, wildlife, range, water, etc.),*** W.B. White, USDA Forest Service, Fort Collins, Colorado

1800- Reception and informal Downeast Clam Bake, University of Maine at Orono. Transportation will be provided.

Wednesday, September 19

0830-1200 *Invitational Papers*
Theme: ***Tactics and strategies for prevention and suppression of damage by spruce budworms***

Moderators: I.W. Varty, Canadian Forestry Service, Maritimes Forest Research Centre, Fredericton, New Brunswick; and W.C. Schmidt, USDA Forest Service, Intermountain Forest and Range Experiment Station, Bozeman, Montana

9. ***Potential silvicultural, harvesting, and salvaging practices in eastern North America,*** B.M. Blum, USDA Forest Service, Northeastern Forest Experiment Station, Orono, Maine
10. ***Forest protection in western North America: the silvicultural approach,*** C.E. Carlson, W.C. Schmidt, and D.G. Fellin, USDA Forest Service, Intermountain Forest and Range Experiment Station; and N.W. Wulf, USDA Forest Service, Clearwater National Forest, Orofino, Idaho
11. ***Tactics and strategies for suppression and prevention of damage,*** J.A. Armstrong, Scientific Advisor, Pesticides, Canadian Forestry Service, Ottawa, Ontario
12. ***Status of biorational agents for controlling the budworms,*** J.C. Cunningham, Canadian Forestry Service, Forest Pest Management Institute, Sault Ste. Marie, Ontario

1300-1700 **Workshop III (Concurrent)—Forest stands and budworms. How do stand types differ in susceptibility and vulnerability and what are the implications for forest management?**

Moderator: W.C. Schmidt

A. ***Characteristics of susceptible/vulnerable stands,*** J.A. Witter, University of Michigan, Ann Arbor, Michigan
B. ***Hazard rating,*** D.G. Fellin, USDA Forest Service, Missoula, Montana
C. ***Silvicultural strategies to reduce susceptibility/vulnerability,*** K.G. Stoszek, University of Idaho, Moscow, Idaho

1300-1700 **Workshop IV (Concurrent)—Techniques of foliage protection and population manipulation. What new or modified techniques are currently available, how effective are they and what developments are in the offing?**

Moderator: I.W. Varty

A. ***Chemicals,*** J.L. Robertson, USDA Forest Service, Berkeley, California
B. ***Biorationals (e.g., microbials, viruses, insect growth regulations, pheromones),*** J.B. Dimond, University of Maine, Orono, Maine
C. ***Applications Technology,*** C.J. Wiesner, New Brunswick Research and Productivity Council, Fredericton, New Brunswick
D. ***Environmental Impact Assessment,*** P.D. Kingsbury, Canadian Forestry Service, Sault Ste. Marie, Ontario

Thursday, September 20

0830-1200 *Invitational Papers*
Theme: ***Integrated forest and pest management, implications for forest management***

Moderator: R.W. Stark, University of Idaho, Moscow, Idaho

13. ***Integrated pest management of spruce budworm in eastern United States,*** G.A. Simmons, Department of Entomology, Michigan State University, East Lansing, Michigan

14. ***Integration of forest and pest management in eastern Canada,*** W. Cuff, Canadian Forestry Service, Maritimes Forest Research Centre, Fredericton, New Brunswick

15. ***Integration of forest pest management: implications for western forest management,*** R. Stage, USDA Forest Service, Intermountain Forest and Range Experiment Station, Moscow, Idaho

1330-1600 *Invitational Panel*

Theme: ***How successful have we been in achieving the goals of the CANUSA program? In meeting the needs of forest management? What remains to be done?***

Chairman: C.R. Blomquist, USDA Forest Service, Eastern Region, Timber Management, Milwaukee, Wisconsin

Participants:

J.C. Mercier, Associate Deputy Minister, Canadian Forestry Service, Ottawa, Ontario

W. Maahs, District Manager, Timberlands International Corp., Milltown, Montana

W.M. Ciesla, Director, USDA Forest Service, Methods Applications Group, Fort Collins, Colorado

R.B. Anderson, Commissioner, Maine Dept. of Conservation, Augusta, Maine

J. Williams, Coordinator–Spruce Budworm Silviculture, International Papers Company, Augusta, Maine

J.R. Carrow, Assistant Deputy Minister, Department of Natural Resources, Fredericton, New Brunswick

1600 *Adjournment*–F.B. Knight

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